ABSTRACT

Title of Dissertation: PLANT MIGRATIONS IMPACT ON POTENTIAL VEGETATION AND CARBON REDISTRIBUTION IN NORTHERN NORTH AMERICA FROM CLIMATE CHANGE.

Steven Anthony Flanagan, Doctor of Philosophy, 2016

Dissertation directed by: Professor. George C. Hurtt, Geographical Sciences

Forests have a prominent role in carbon storage and sequestration. Anthropogenic forcing has the potential to accelerate climate change and alter the distribution of forests. How forests redistribute spatially and temporally in response to climate change can alter their carbon sequestration potential. The driving question for this research was: How does plant migration from climate change impact vegetation distribution and carbon sequestration potential over continental scales? Large-scale simulation of the equilibrium response of vegetation and carbon from future climate change has shown relatively modest net gains in sequestration potential, but studies of the transient response has been limited to the sub-continent or landscape scale. The transient response depends on fine scale processes such as competition, disturbance, landscape characteristics, dispersal, and other factors, which makes it computational prohibitive at large domain sizes. To address this, this research used an advanced

mechanistic model (Ecosystem Demography Model, ED) that is individually based, but pseudo-spatial, that reduces computational intensity while maintaining the fine scale processes that drive the transient response. First, the model was validated against remote sensing data for current plant functional type distribution in northern North America with a current climatology, and then a future climatology was used to predict the potential equilibrium redistribution of vegetation and carbon from future climate change. Next, to enable transient calculations, a method was developed to simulate the spatially explicit process of dispersal in pseudo-spatial modeling frameworks. Finally, the new dispersal sub-model was implemented in the mechanistic ecosystem model, and a model experimental design was designed and completed to estimate the transient response of vegetation and carbon to climate change. The potential equilibrium forest response to future climate change was found to be large, with large gross changes in distribution of plant functional types and comparatively smaller changes in net carbon sequestration potential for the region. However, the transient response was found to be on the order of centuries, and to depend strongly on disturbance rates and dispersal distances. Future work should explore the impact of species-specific disturbance and dispersal rates, landscape fragmentation, and other processes that influence migration rates and have been simulated at the sub-continent scale, but now at continental scales, and explore a range of alternative future climate scenarios as they continue to be developed.

PLANT MIGRATIONS IMPACT ON POTENTIAL VEGETATION AND CARBON REDISTRIBUTION IN NORTHERN NORTH AMERICA FROM CLIMATE CHANGE.

by

Steven Anthony Flanagan

Dissertation submitted to the Faculty of the Graduate School of the
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Dedication

For my parents: Mimi Flanagan and Steve Flanagan Sr.

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Chapter 1: Introduction

1.1 Motivation and Background

Forests have a prominent role in the carbon balance as they sequester approximately 30% of annual fossil fuel emissions and contain roughly 80% of the above ground carbon (Bonan, 2008; Goulden et al., 1996). Anthropogenic forcing is expected to change climate at its greatest rate in the next century (Houghton & Woodwell, 1989; Vitousek et al., 1997). An anticipated consequence of anthropogenic climate change is the redistribution of forests, and hence their carbon sequestration potential, as supported by paleoclimatology records from pollen studies (Davis, 1969; Davis & Botkin, 1985; Firbas & Losert, 1949). The transient response of vegetation to climate change is an under-represented process in large domain simulations as it is computationally prohibitive to simulate this fine scale process above the landscape, or subcontinent scale (J. S. Clark et al., 2011b; Lischke et al., 2006; McKenney et al., 2007).

The equilibrium response is predicted with climate-ecosystem relationships and the use of dynamic global vegetation models (DGVMs). Emanuel *et al.* used a Holdridge Life-Zone Classification scheme with elevated CO_2 to simulate global changes in temperature provided by a General Circulation Model (GCM), and predicted forest expansion north with increased grassland and desert at lower latitudes (Emanuel et al., 1985). GCMs combined with plant functional types (PFTs) were use to map the spatial fraction of tree types under current climate and with doubled CO_2 (Brovkin et al., 1997). To move beyond mapping predicted redistribution patterns

and fractions of trees, DGVMs are used as they include representations of establishment, mortality, and competition (Pitelka, 1997). Bachelet *et al.* used both an equilibrium model (the Mapped Atmosphere-Plant-Soil System, MAPSS, model) and a DGVM (MC1) under 7 different GCM climate change scenarios for the US to track changes in forest and biomass (Bachelet et al., 2001) and found small increases in temperature resulted in increased carbon sequestration while larger changes produced loses. Schapoff *et al.* used one emission scenario with five GCMS and the LPJ-DGVM and found global changes in carbon by the end of the century ranged from -106 to +201 PgC, with three scenarios producing a land carbon source, one neutral, and one a sink (Schaphoff et al., 2006). The magnitude and sign of these experiments supports, and calls for, the impact that the transient response of vegetation migrating will have on the total carbon sequestration potential (Neilson et al., 2005; Pereira et al., 2010; Pitelka, 1997) as rapid climate change needs rapid migration or the predicted equilibrium sequestration potential is altered.

The transient response depends on fine scale processes such as competition, disturbance, landscape characteristics, dispersal, and other processes (Kuchler, 1973; Collingham & Huntley, 2000; Plotnik & Gardner, 2002; Renton et al., 2013). Transient dynamics of the forest community, such as landscape heterogeneity and disturbance regimes, influence migration rates (Sykes & Prentice, 1995; Thomas et al., 2008). Disturbance and landuse history are closely linked as migration rates are confined by both natural and human induced changes in land cover (Hurtt et al., 1998; Medvigy & Moorcroft, 2012) and have been shown to both accelerate and impede migration rates (J. S. Clark et al., 1998; Dale et al., 2001; Midgley et al., 2007;

Theoharides & Dukes, 2007) SORTIE is a mechanistic model that contains sub models that predict growth, probability of survival, production of recruits, and resource availability for individuals in a stand (Ribbens et al., 1994). Ten tree species characteristics with different recruitment characteristics were examined and changes in species abundance from climate change were observed. DISTRIB and SHIFT are two other models that when combined simulate migration and consider landscape fragmentation (Iverson et al., 2004). DISTRIB is a statistical model that simulates future suitable habitat under climate change while SHIFT is a cellular automata model that estimates migration based on the abundance of a species near a boundary. Results showed a potential lag in species establishment.

Currently, the two main approaches to simulate the transient response over large domains are to use a top-down approach or a representative forest. The Joint UK Land Environment simulator (JULES) is a process-based model that simulates land surface-atmosphere interactions (D. B. Clark et al., 2011a; Fisher et al., 2010) and uses the Top-down Representation of the Interactive Foliage and Flora Including Dynamics (TRIFFID) for its vegetation dynamics (Cox, 2001). Top-down means it uses land-surface characteristics such as vegetated fraction and leaf area index to model vegetation dynamics at a site. Hence, it is driven by a number of empirical equations and can be used at large scales while not being computational intensive, but is not individually based so explicit migration between cells does not occur. Rather, a portion of every plant functional type always exists in every cell and the resident vegetation impedes establishment of new species.

For explicit migration, forest gap models are used. Gap models simulate complex interactions but their spatially explicit nature often limits their domain size. One of the more advanced gap models is TreeMig, which operates at the stand to landscape (subcontinent) scale (Lavorel et al., 1997; Lischke et al., 2006). It accounts for within-cell heterogeneity of the 30 most important Central European species and includes such forest dynamic aspects as growth, competition, mortality, seed production, seed bank dynamics, dispersal, germination, and sapling developing. It operates with dispersal kernels that allow for short and long distance dispersal and its shading mechanism generates a height based heterogenic landscape within each cell. However, the fact that it is spatially explicit and generally operates on a 1km by 1km scale means it is computationally prohibitive to move beyond the subcontinent scale.

Extensive studies have also been performed in the US using gap models. LANDIS-II is a spatially explicit landscape model that simulates successional processes, including disturbance and seed dispersal (Duveneck et al., 2014; Scheller et al., 2007). It was used to study climate change effects on the Great Lake forests in regards to preserving diversity under three climate change scenarios and found that maintaining diversity is important in enabling the adaptive capacity of forests. Its cell size ranges from a few meters up to a kilometer. LANDIS PRO is from the same family of models and has been used in the Northeast, Central Appalachian, and Central Hardwood regions of the US, with a planned study in the Gulf Coastal Plain (Wang et al., 2014). The model can be directly initialized, calibrated, and validated

with FIA data and explores successional dynamics, but again is limited to the landscape scale as its resolution is typically 90-270m.

To make use of the desired mechanistic properties these models contain while also moving to a larger domain a representative forest can be used. Scaling up an explicit forest to a representative area to simulate migration over a larger domain is a process most recently undertaken in the SEIB-DGVM model (Sato & Ise, 2012; Sato et al., 2007). The model uses a 30m x 30m spatially explicit forest similar to the one in TreeMig, but extrapolates the results to a 0.5 x 0.5 degree area. As the explicit forest is orders of magnitude smaller than the domain it represents, dispersal kernels are removed and the maximum dispersal distance in the literature, which is 100km per century (Woodall et al., 2009), used. Disturbance was found to be necessary for rapid plant migration as resident species largely prevent the establishment of species presumed to be better adapted to the new environment predicted by climate change scenarios (Sato et al., 2007). But by scaling the explicit forest, more complex dispersal strategies needed to be discarded and only unlimited or no migration was simulated.

An alterative method to simulating the transient response of vegetation and carbon to climate change, but at larger domain sizes, is to use a pseudo-spatial model, such as the Ecosystem Demography (ED) model (Hurtt et al., 1998; Moorcroft et al., 2001). ED is an individual tree based model that uses a size and age-structured approximation for the first moment of the stochastic (gap) ecosystem model. It contains integrated sub-models of plant growth, mortality, phenology, biodiversity, disturbance and soil biogeochemistry with plants, represented as PFTs, competing for

light, water, and other nutrients. By scaling up physiological processes through individual-based vegetation dynamics to ecosystem scales, it reduces the computational requirements of large domain simulations. It has been implemented in South, Central, and North America, as well as the US, and will be used in the upcoming NASA GEDI mission (Albani et al., 2006; Hurtt et al., 2002; Moorcroft et al., 2001, Flanagan et al., 2016). The driving question then becomes: How do we represent the spatially explicit process of dispersal in a pseudo-spatial framework and then what is plant migrations impact on potential vegetation and carbon redistribution from climate change at large domain scales? The end result is the first model we know about capable of doing large domain simulations of plant migration using an individual based model that is necessary for dispersal characteristics.

1.2 Research Overview

Thus, the ultimate goal of my research was to analyze how plant migration from climate change impacted vegetation distribution and carbon sequestration potential over continental scales. To do so, I calibrated the ED model to match remote sensing data on the distribution of dominant PFTs in northern North America under current climate conditions. A future climatology was then used to predict the potential equilibrium vegetation and carbon distribution from climate change. A theoretical function for pseudo-spatial migration was developed and validated with the use of idealized simple simulators. The migration function was implemented in ED, and various scenarios were run to determine the impact of the transient response

of plant migration on future vegetation and carbon redistribution from climate change.

The major objectives were:

- Calibrated the ED model to match remote sensing data on the current distribution of dominant PFTs in northern North America and used a future climatology to predict the equilibrium response of vegetation and carbon.
- Developed and validated a theoretical equation for pseudo-spatial migration.
- Used the pseudo-spatial migration sub-model in ED and ran a model experimental design with different dispersal rates, dispersal modes, and disturbance rates and predicted the potential impact of plant migration on vegetation distribution and carbon sequestration potential from future climate change.

The three research components of the dissertation combined to present a method for exploring the transient response of vegetation from migration at continental scales, and the corresponding impact this had on carbon sequestration potential. First, in Chapter 2, I explored the equilibrium response of vegetation to climate change. I found that large changes in local vegetation and carbon distribution resulted in modest net gains in carbon sequestration potential.. The size of the domain predicted to change dominant PFT, and the trends of northern expansion of the boreal forest and deciduous migration into habitat currently classified as evergreen, demonstrated the transient response should be simulated. Therefore, in

Chapter 3, I used idealized simulators of explicit and pseudo-spatial migration to develop an intuitive theoretical representation of migration in a pseudo-spatial environment and tested that it produced reasonable results for unoccupied habitat in ED. In Chapter 4, I used ED with the developed migration sub-model to conduct a model experimental design with various dispersal distances, dispersal modes, and disturbance rates and determined the potential impact that plant migration from future climate change had on vegetation distribution and carbon sequestration potential. Finally, in Chapter 5, the general results, summary of findings, and future research areas are addressed.

Chapter 2: Potential Vegetation and Carbon Redistribution in Northern North America from Climate Change

2.1 Abstract

There are strong relationships between climate and ecosystems. With the prospect of anthropogenic forcing accelerating climate change, there is a need to understand how terrestrial vegetation responds to this change as it influences the carbon balance. Previous studies have primarily addressed this question using empirically based models relating the observed pattern of vegetation and climate, together with scenarios of potential future climate change, to predict how vegetation may redistribute. Unlike previous studies, here we use an advanced mechanistic, individually based, ecosystem model to predict the terrestrial vegetation response from future climate change. The use of such a model opens up opportunities to test with remote sensing data, and the possibility of simulating the transient response to climate change over large domains. The model was first run with a current climatology at half-degree resolution and compared to remote sensing data on dominant plant functional types for northern North America for validation. Future climate data were then used as inputs to predict the equilibrium response of vegetation in terms of dominant plant functional type and carbon redistribution. At the domain scale, total forest cover changed by ~2% and total carbon storage increased by ~8% in response to climate change. These domain level changes were the result of much larger gross changes within the domain. Evergreen forest cover

decreased 48% and deciduous forest cover increased 77%. The dominant plant functional type changed on 58% of the sites, while total carbon in deciduous vegetation increased 107% and evergreen vegetation decreased 31%. The percent of terrestrial carbon from deciduous and evergreen plant functional types changed from 27%/73% under current climate conditions, to 54%/46% under future climate conditions. These large predicted changes in vegetation and carbon in response to future climate change are comparable to previous empirically based estimates, and motivate the need for future development with this mechanistic model to estimate the transient response to future climate changes.

2.2 Introduction

Previous research has demonstrated a strong relationship between climate and the distribution of terrestrial ecosystems (Holdrige, 1947; Köppen, 1900; Thornthwaite, 1931; 1948), and anthropogenic forcing is expected to change future climate at its greatest rate in the next century (Dale et al., 2001; Gruber & Galloway, 2008; Houghton & Woodwell, 1989; Matear, et al., 2010; Vitousek et al., 1997). Forests have important biophysical and biogeochemical properties relevant to climate and, contain roughly 80% of above ground carbon and sequester approximately 30% of annual fossil fuel carbon emissions (Bonan, 2008). Therefore, how terrestrial ecosystems respond to future climate and the carbon consequences associated with this change are important research topics (Bonan, 2008; Goetz & Dubayah, 2011; Goulden et al., 1996).

The potential equilibrium response of vegetation to climate change has previously been estimated using empirically derived climate-ecosystem relationships (Köppen, 1900; Thornthwaite, 1931; 1948). Köppen used a classification system based on temperature, evapotranspiration rate, seasonality of precipitation, and severity of dry season to predict ecosystem type (Köppen, 1900). Holdrige's diagram is considered the most iconic climate-ecosystem classification scheme and produced an ecosystem classification key based on temperature, precipitation, and evapotranspiration (Holdrige, 1947). Thornthwaite used the variables precipitation effectiveness and temperature efficiency, based strongly on transpiration, to generate eight major climate regions (Thornthwaite, 1931; 1948). When given a climate change scenario, these empirical schemes have been used to map potential future ecosystem distributions (Neilson et al., 2005; K. C. Prentice & Fung, 1990). Moreover, using two climate data sets, Prentice found that they could replicate ~80% of the observed land surface before predicting future distribution from climate change (K. C. Prentice, 1990).

While equilibrium response of vegetation to climate is important, the transient response is also important, potentially introducing lags in response, novel communities, and other patterns (J. S. Clark et al., 1998; Pacala & Hurtt, 1993.). Estimation of these transient responses requires the use of mechanistic models able to predict the consequences of limited and varied dispersal, plant competition, and other factors. Generally, progress applying such models to this problem is limited. TreeMig is one of the more advanced mechanistic gap models (Lischke et al., 2006). It accounts for within-cell heterogeneity of the 30 most important Central European

species and includes such forest dynamic aspects as growth, competition, mortality, seed production, seed bank dynamics, dispersal, germination, and sapling development. TRIFFID is a process-based model that uses a top-down approach ideal for large domain simulations, and can simulate land-surface interactions when coupled with JULES (D. B. Clark et al., 2011a; Cox, 2001). SEIB-DGVM is a spatially explicit forest model that scales up to a larger domain to research the transient response (Sato et al., 2007; Sato & Ise, 2012). Despite this progress, additional work is needed to examine the transient response mechanistically over large domains.

Here we used an advanced individually based mechanistic ecosystem model that is formulated to overcome many of these limitations, and applied it to predict the response of vegetation and carbon to future climate over northern North America. As implemented, the model is pseudo-spatial, which decreases computation time while retaining individually based formulation. Specifically, this study (1) validated model predicted dominant plant functional type (PFT) distribution in northern North America under current climate conditions through a comparison with remote sensing data and (2) used a future climate change scenario as input to simulate the equilibrium response of the expected redistribution of dominant PFTs and carbon.

2.3 Methodology

2.3.1 Model

The Ecosystem Demography (ED) model (Hurtt et al., 1998; Moorcroft et al., 2001) is an individual tree based model that uses a size and age-structured approximation for the first moment of the underlying spatial stochastic process of

vegetation dynamics. ED differs from most terrestrial models by using a size-age-structure approximation of the first moment of the stochastic simulator to scale. Thus it is an individual-based model of vegetation dynamics with submodels of growth, mortality, water, phenology, biodiversity, disturbance, hydrology, and soil biogeochemistry. Individual PFTs compete mechanistically for water, nutrients, and light. It has been successfully implemented in South and Central America, the United States, and is currently being used in NASA's Carbon Monitoring System (Hurtt et al., 2015) and the upcoming NASA mission GEDI.

Plants in ED are represented by PFTs, which partition vegetation into discrete classes defined by physiognomy, leaf habitat, photosynthetic pathway, leaf form, and other characteristics (Foley et al., 1996; Haxeltine & Prentice, 1996; I. C. Prentice et al., 1992). Following Hurtt *et al.* 2002 (Hurtt et al., 2002), trees in North America were represented by two dominant types, cold deciduous and evergreen. ED was modified from its previous implementation over the U.S. for high latitudes (R. Q. Thomas et al., 2008), and to improve down regulation of carboxylation rates as available light decreases on descending the vertical canopy for each PFT. The maximum carboxylation rate for evergreen was set to 9 $\mu mols \cdot m^{-2} \cdot s^{-1}$ and deciduous to 7 $\mu mols \cdot m^{-2} \cdot s^{-1}$ which is consistent with literature values (Caemmerer & Farquhar, 1981; Farquhar & Sharkey, 1982; Foley et al., 1996).

ED was then run for 500 years with current climate data in the domain of northern North America (40°N to 75°N and 165°W to 50°W) to establish the predicted current dominant PFT. The average year of the entire dataset (1901–2010) was used as the driver. Dominant PFT was determined by applying the National Land

Cover Dataset 1992 (NLCD92) (Vogelmann et al., 2001) forest classification definitions of deciduous, evergreen, and mixed forests to the output. These definitions call for 25% of a site to have tree cover to be classified a forest, and greater than 75% of that cover to be a specific type to not be considered a mixed forest. ED was then run with a future climatology over the same domain using the average of the last five years of the dataset (2065–2070). The model was run for 500 years and the NLCD92 classification applied as in the previous part. A comparison between current and future dominant PFT showed the percentage of sites expected to convert type and the specific conversions (*i.e.*, evergreen becomes deciduous forest, non-forest becomes evergreen).

2.3.2 Climate Data

Two climate datasets were used. A current climate dataset to initialize the model to contemporary conditions and compare model predictions of dominant PFT against remote sensing data, and a future climate dataset for use as input to simulate future ecosystem dynamics and redistribution of dominant types. Increases in resolution improve the ability to adequately capture all aspects of forest dynamics (Hurtt et al., 2010), so the highest resolution climate change data set available with the inputs necessary to drive ED was chosen. The climate attributes that drive ED are specific humidity, surface temperature, precipitation, and photosynthetically active radiation. Though new climate change datasets are constantly produced they often do not contain the specific humidity data ED requires. For contemporary conditions, the North America Carbon Program (NACP) data set from the Multi-Scale Synthesis and Terrestrial Model Intercomparison Project (MsTMIP) was used (Wei et al., 1994;

2013). This data is referred to as CRUNCEP and is a combination of the Climate Research Unit (CRU) and National Centers for Environmental Prediction (NCEP) climatologies. CRUNCEP is a global 0.5 × 0.5 degree climatology with a 6 h daily time step from 1901–2010 in a WGS84 projection.

For the future, the North American Climate Change Assessment Program (NARRCAP) produces multiple future climatologies with required attributes at ~50 km resolution (Mearns et al., 2009). NARCCAP provides climate change projections by coupling a set of regional climate models (RCMs) driven by a set of atmosphere-ocean general circulation models (AOGCMs) that are forced with the Special Report on Emission Scenarios (SRES) A2 scenario for the 21st century, which has atmospheric carbon increasing to 575 ppm by mid-century. The combination of the Community Climate System Model (CCSM) as the driving model and MM5I as the regional model was used. It contains future climate data for 2041–2070 at ~50 km resolution with 3 h daily times steps in a Lambert Conic Conformal projection. The NARCCAP climatology was converted to half-degree resolution with a WGS84 projection to match the CRUNCEP climatology.

2.3.3 Remote Sensing Data

Remote sensing and field data have provided a valuable resource in constraining ecosystem models (Hurtt et al., 2004). To determine PFT distribution from remote sensing data the AVHRR Continuous Fields Tree Cover Product (CFTCP) produced by Global Land Cover Facility (GLCF) was used (DeFries et al., 1992). The product contains percent deciduous, coniferous, and total tree cover layers at 1 km resolution. CFTCP was averaged to 0.5 × 0.5 degree resolution to match the resolution of the

climatologies and the NLCD92 classification that was applied to the model outputs used to generate a dominant PFT distribution from remote sensing under current climate conditions. The PFT distribution from current climate predicted by the model was validated against the remote sensing distribution.

2.4 Results

2.4.1 Dominant Plant Functional Type Distribution

The comparison of the distribution of the dominant PFT (evergreen or deciduous) in northern North America between remote sensing data and model prediction is presented in Figure 2.1. Despite considerable agreement, differences arise in this comparison because of fundamental difference between the remote sensing product (actual) and ED (potential) treatment of forest. To gain the fairest comparison, we restricted our analysis to sites determined to be forest by remote sensing data. In 76% of the 3064 forested sites that met this criteria, model prediction of dominant PFT and remote sensing data were in agreement (Figure 2.1). By remote sensing, this area was comprised of 77% evergreen, 16% mixed, and 7% deciduous. Model prediction over this area was 74% evergreen, 26% deciduous, and less than 1% mixed. ED supported mixed forests sites, and a cluster exists around 45°N 110°W, but typically produced a prevalence of one dominant PFT per site. Therefore, the mixed forest boundary between deciduous and evergreen forests that appears in the remote sensing data was under represented in the model output. However, when mixed forest was considered a transition zone in the model, essentially combining the deciduous and mixed PFTs, the agreement increased to 82% (Figure 2.2).

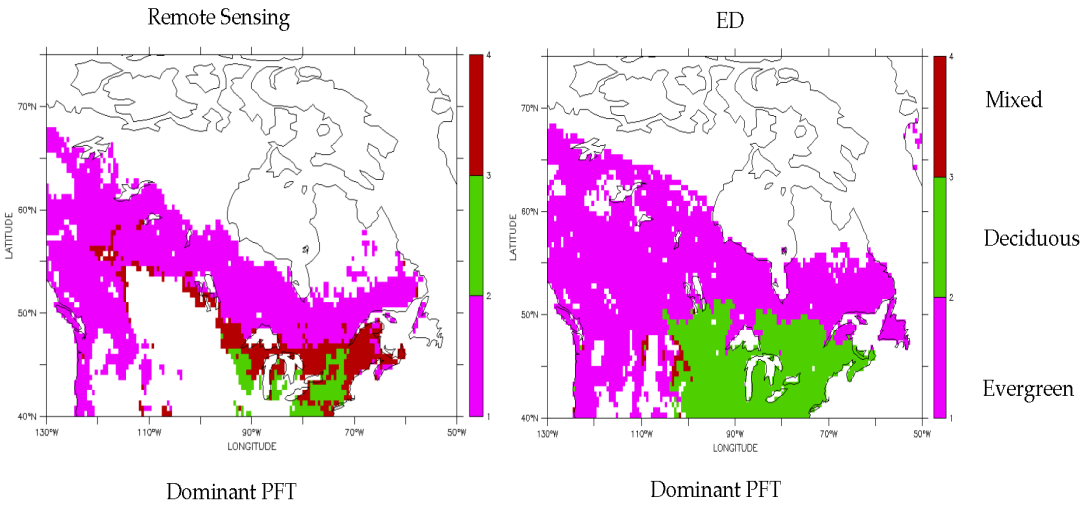

Figure 2.1. Dominant PFT distribution from remote sensing data (**left**); and model prediction (**right**) from current climate.

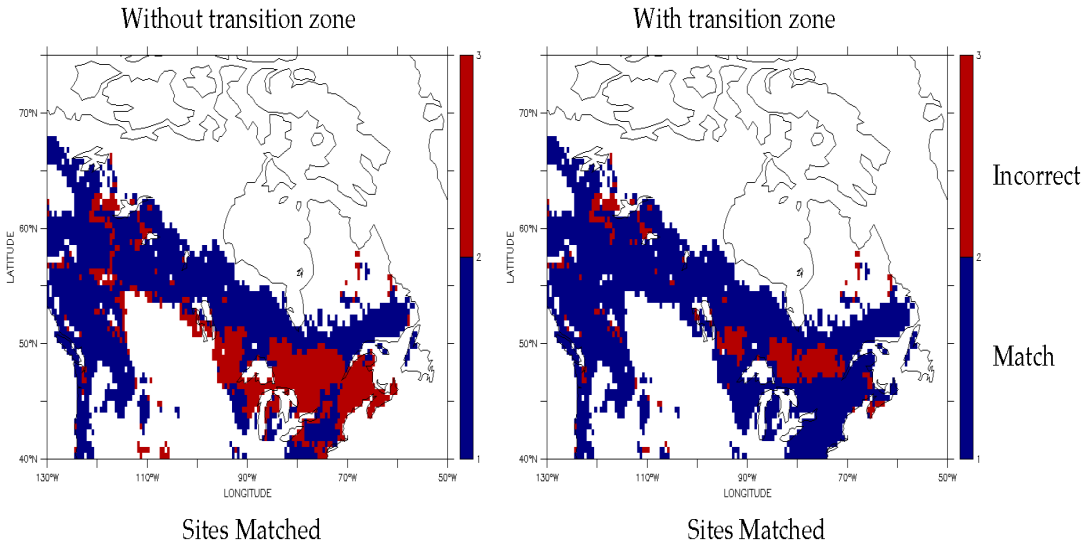

Figure 2.2. Areas of agreement (blue) and disagreement (red) without (**left**) and with (**right**) the mixed forest considered a transition zone.

2.4.2 Predicted Dominant Plant Functional Type Redistribution from Climate Change

The predictions of dominant PFT distributions based on current climate were next compared to those based on future climate (Figure 2.3).

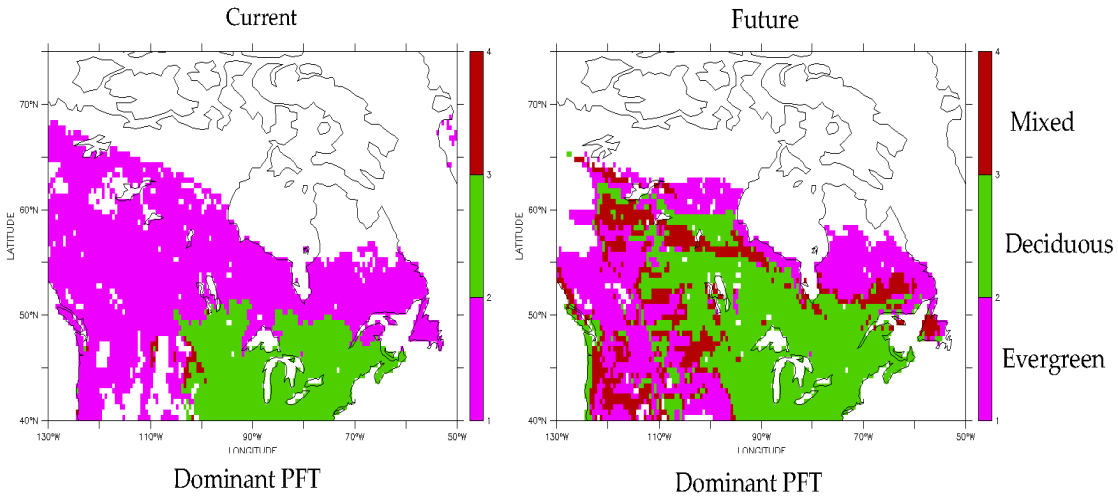

Figure 2.3. Contemporary and future predictions for mixed, deciduous, evergreen, and non-forest PFTs.

Under future climate conditions, total forest cover increased from 4764 sites to 4839 sites, a 2% increase. Deciduous sites increased from 1223 to 2159 sites, a 77% increase, while evergreen sites decreased from 3497 to 1811 sites, a 48% decrease. Overall, 58% of the domain changed dominant PFT (Figure 2.4). All the transitions between PFTs and non-forest were tracked, but evergreen expansion and withdrawal accounted for ~90% of the predicted change (Table 2.1). The transitions are shown with a dominant PFT change map (Figure 2.5).

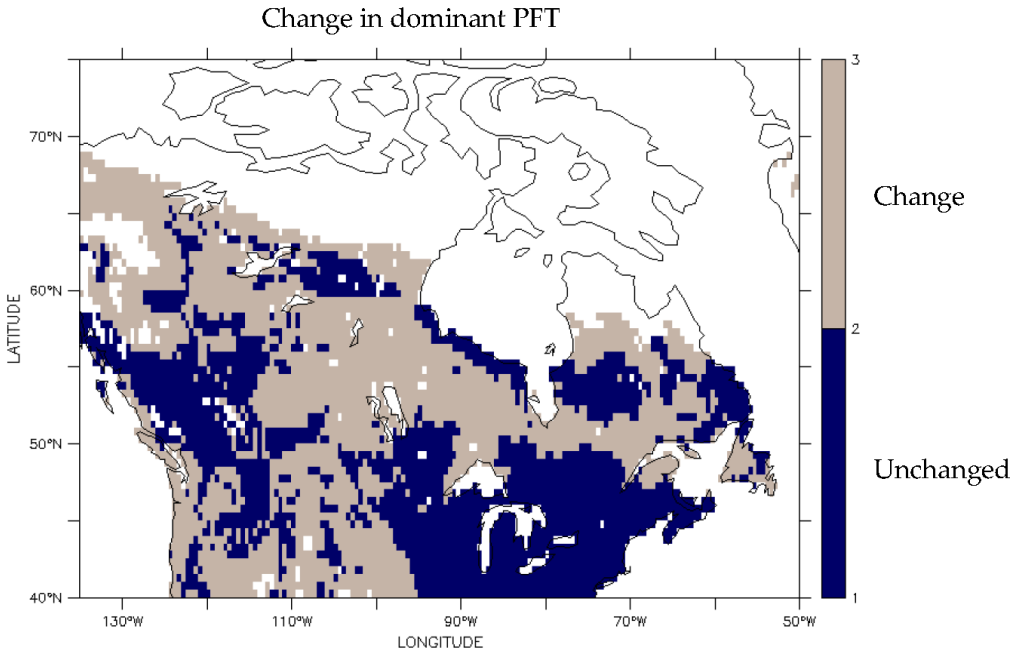

Figure 2.4. Sites that switch dominant PFT (gray) and remain unchanged (blue).

Dominant plant functional type change	Percentage of sites in domain
Evergreen turns into deciduous	21
Evergreen turns into mixed	15
Non-forest turns into evergreen	8
Evergreen turns into non-forest	7
Deciduous turns into evergreen	2
Mixed turns into evergreen	>1

Table 2.1. Percentage of sites in the domain that had either evergreen expansion or withdrawal. These changes accounted for 58% of the total 60% change in dominant PFT predicted.

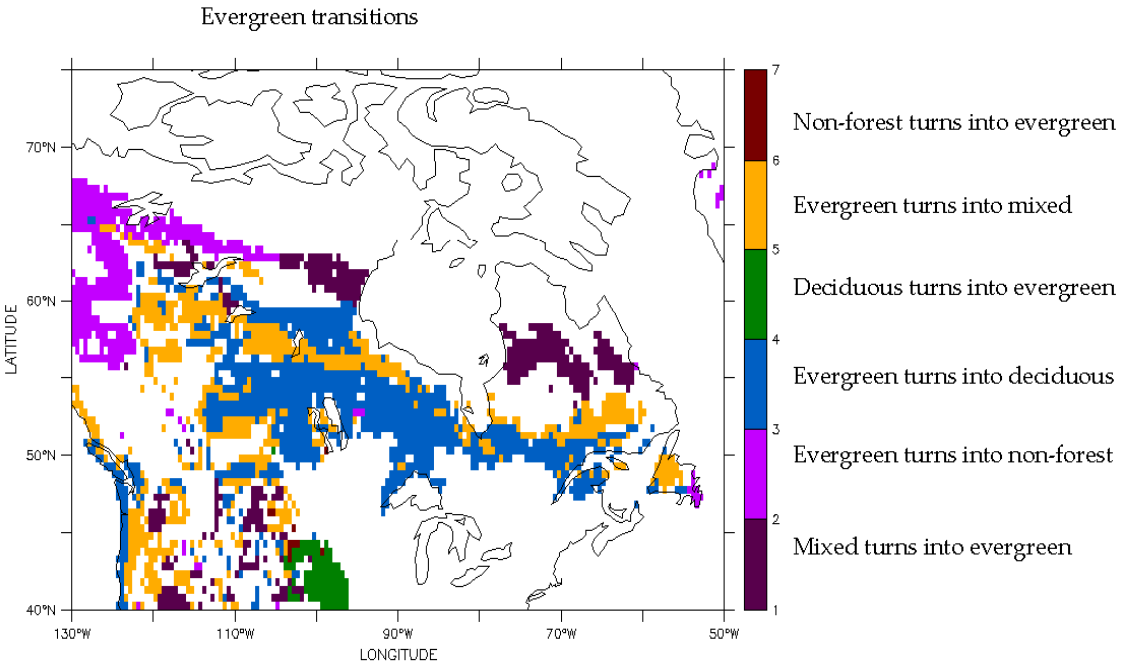

Figure 2.5. Predicted evergreen transitions of dominant plant functional from climate change.

2.4.3 Implications for Carbon Redistribution and Change

The predicted redistribution of PFTs has implications for carbon stocks (Table 2.2) and fluxes (Table 2.3).

Carbon (Tg)				
Carbon Type	**Current**	**Future**	**Difference**	**Percent Change**
Total	54	58	4	8
Deciduous	15	31	16	107
Evergreen	39	27	−12	−31

Table 2.2. Carbon amount, difference, and percent change predicted by ED for current and future climate.

Percentage of Total Carbon		
Scenario	**Deciduous**	**Evergreen**
Current	28	72
Future	54	46

Table 2.3. Percentage of total carbon comprised of deciduous and evergreen from current and future climate.

In response to climate change, total carbon across the domain increased 8%. This aggregate increase was a combined result of an increase in deciduous carbon and decrease in evergreen carbon. Total terrestrial carbon increased 4 Tg (8%), deciduous carbon increased 16 Tg (107%), and evergreen carbon decreased 12 Tg (31%). In terms of percentage of carbon by PFT, deciduous carbon increased from 28% to 54%, and evergreen carbon decreased from 72% to 46%. Though regional total carbon increases are relatively modest, the underlying gridded changes were larger and had a wide distribution (Figure 2.6), and differed by PFT (Figure 2.7).

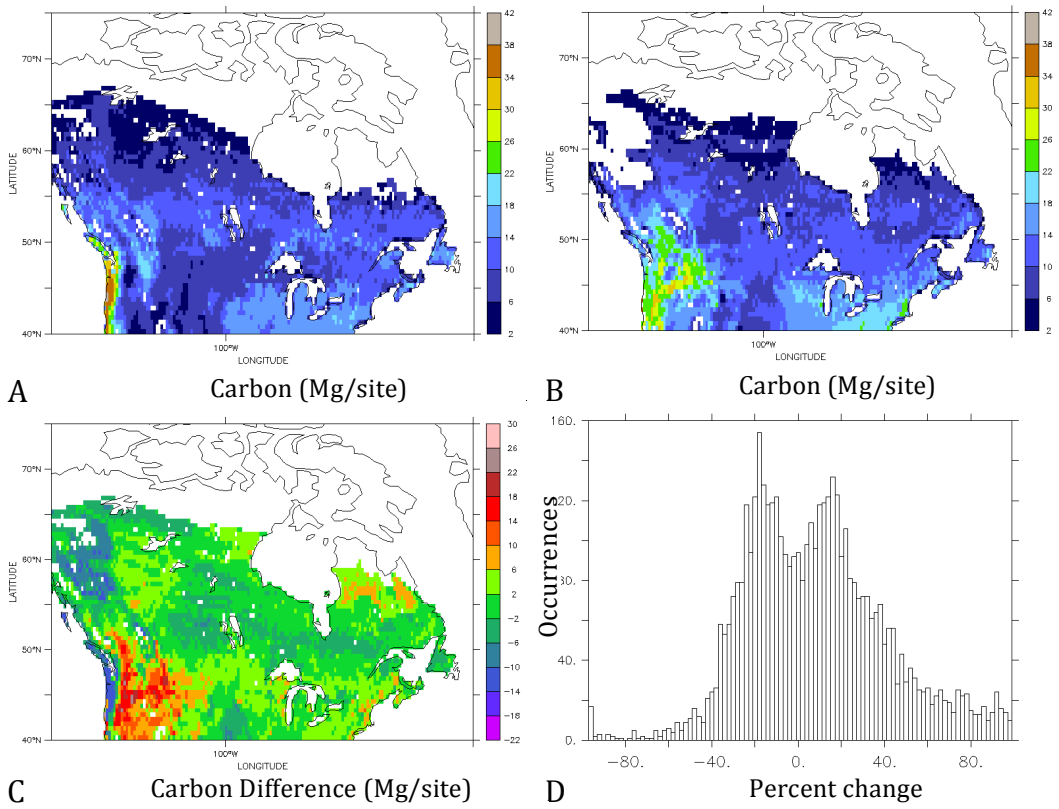

Figure 2.6. Predicted total carbon under (**A**) current climate and (**B**) future climate; (**C**) The carbon difference between the current and future; and (**D**) the percent change in carbon distribution.

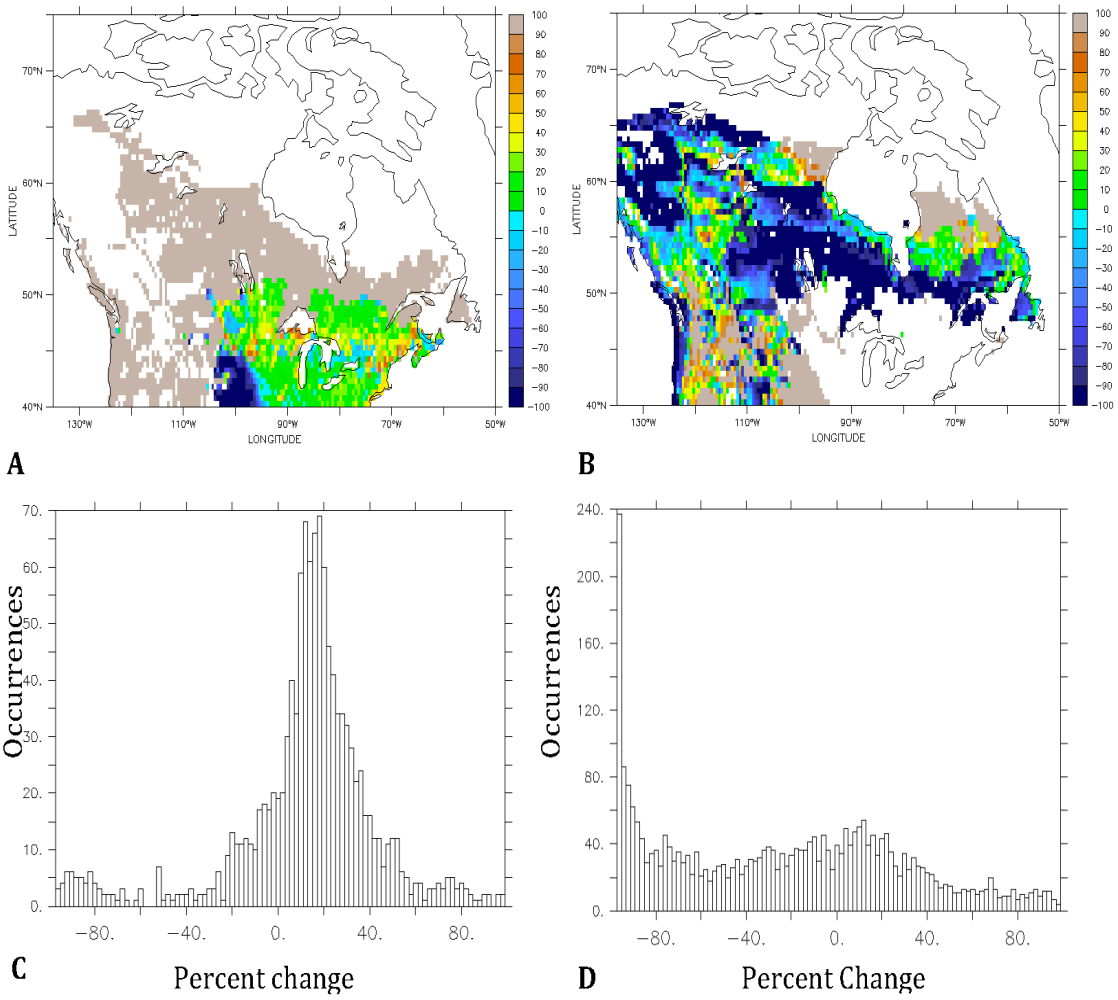

Figure 2.7. The percent change in (**A**) deciduous; and (**B**) evergreen terrestrial carbon from climate change, and histograms of the percent change occurrences (**C**,**D**).

2.5 Discussion

This study used an advanced mechanistic ecosystem model and future climate scenario to estimate the potential equilibrium response of vegetation and carbon to future climate change over North America. Results suggest a relatively modest net domain level change in both forest cover and carbon, with much larger underlying gridded changes in both the distribution of vegetation and carbon stocks. Total forest

cover expanded 2% and total carbon storage increased 8% (4 Tg). Underlying these regional net changes, deciduous cover expanded by 77% and gained 107% carbon (16 Tg), while evergreen cover was reduced by 48% and lost 31% carbon (12 Tg). In all, nearly 60% of the domain was shown to expect to change dominant PFT, with the percentage of terrestrial carbon attributed from evergreen and deciduous PFTs to change from a 1:3 to 1:1 ratio with wide ranges in carbon storage fluctuations at the site level. Such changes have potentially large climate, biogeochemical, and other implications.

Like previous studies, this work focused on estimating the long-term equilibrium response of vegetation and carbon to climate change. However, unlike previous studies based on empirical climate-vegetation models, this study used an advanced mechanistic, individually based ecosystem model. The use of such a model allowed for large domain validation of dominant PFT distribution from remote sensing data (Figure 2.2), and potential future opportunities to utilize additional remote sensing data as well as simulating the transient response of vegetation and carbon to climate change over large domains. Our results here are comparable to previous studies of vegetation and terrestrial carbon equilibrium response to climate change. For example, Schaphoff *et al.* (Schaphoff et al., 2006) used the LPJ-DGVM model with five different climate change projections and found vegetation carbon to increase 7.7% on average globally, but with differing response in vegetation patterns. Solomon and Kirilenko (Kirilenko & Solomon, 1998) doubled CO_2 globally and found a relatively modest response in net carbon gains with underlying biome changes exhibiting larger changes, similar to the findings we present.

For the northern hemisphere, the predicted underlying changes are evergreen forest replaced by deciduous forest at the southern boundary but expanding at the northern boundary. Rehfledt *et al*. (Rehfeldt & Tchebakova, 2002; Rehfeldt et al., 2006; Rehfeldt et al., 1999) provides a number of empirical based studies on multiple species under altered climate change scenarios in the western United States that are consistent with these results. Sykes and Prentice (Sykes & Prentice, 1995) doubled CO_2 and found that boreal species withdraw northward as temperate deciduous species dramatically expand into boreal tracts. Additional studies have focused on transitional zones, regions that are expected to change ecosystem type from climate change. These studies include regions such as those at high latitudes where boreal forest zones are replaced by cool temperate forest or cool temperate steppe (Emanuel et al., 1985), taiga to tundra migration (Montesano et al., 2009; Ranson et al., 2004), and deciduous forests northward expansion (Chapin et al., 2010). Based on these studies, boreal forests are projected to temporarily become a carbon source as deciduous forests are expected to move northward, but only after evergreen withdrawal (Ranson et al., 2004), while the artic becomes a sink as boreal species migrate into regions previously classified as tundra (Chapin et al., 2010; Emanuel et al., 1985; Montesano et al., 2009; Ranson et al., 2004). Our results project evergreen forests moving into higher latitudes (Grace, 2002; Ranson et al., 2004; Soja et al., 2007), and deciduous forests moving into areas previous classified as evergreen (Goldblum & Rigg, 2005). These changes at the PFT level (Figure 2.5) likely mask larger and more complex underlying changes at the species level. As the functional type representation of biodiversity is aggregated, it does not track species level shifts.

Large potential changes in response to climate change has lead scientists to examine the transient response (Bachelet et al., 2001; Iverson et al., 2004; Medvigy & Moorcroft, 2012; Montesano et al., 2009; Neilson et al., 2005; Sato & Ise, 2012). The transient response of vegetation to climate change may introduce a time-lag to equilibrium as species have withdrawal-invasion interactions dependent on the climate change rate that can influence terrestrial carbon stocks. Research on the transient response must include additional submodels of landscape characteristics, disturbance rates, dispersal properties, and how these factors might be altered with climate change (Bailey, 1983; Collingham & Huntley, 2000; Küchler, 1973; Lavorel et al., 1997; Pitelka, 1997; Plotnick & Gardner, 2002; K. C. Prentice, 1990; Sykes & Prentice 1995). Disturbance has been found to be necessary for rapid plant migration as resident species largely prevent the establishment of species presumed to be better adapted to the new environment predicted by climate change scenarios (Sato et al., 2007), but too much disturbance prevents new species establishment (Denslow, 1980; Sykes & Prentice, 1995). Landscape heterogeneity and habitat fragmentation can both accelerate and retard plant migration rates (Collingham & Huntley, 2000; Fahrig, 2002; Küchler, 1973; Pitelka, 1997; Svenning & Skov, 2004), and dispersal kernels should be used to vary the speed of dispersal and migration dependent on species type to account for Reid's paradox (J. S. Clark et al., 1998; Kot et al., 1996; Lischke et al., 2006; Peel et al.,2007). With rapid climate change rapid tree migration rates must occur or species face extinction and alter the expected carbon balance as the equilibrium state does not have enough time to establish (Iverson et al., 2004; Lenoir et al., 2008; Midgleyet al., 2007; Neilson et al., 2005; Peñuelas et al., 2007).

The computational requirement for simulating theses interactions often limits the domain size to the subcontinent scale (Lavorel et al., 1997; Lischke et al., 2006). Extensive work on the risk and vulnerability of forests to climate change has been done for the eastern United States (Duveneck et al., 2014; Iverson et al., 2004; Iverson et al., 2011; Iverson et al., 2007; Matthews et al., 2014; Zolkos et al., 2015). Two models, DISTRIB and SHIFT, were combined to estimate the potential migration of five tree species in the eastern U.S. from climate change in the next 100 years (Iverson et al., 2004). DISTRIB used a statistical approach to predict suitable habitat from climate while SHIFT provided the probability of colonization and coupled they showed the proportion of new habitat colonized within a century was low for all species under multiple climate change scenarios. Subsequent research illustrated large potential changes in suitable habitat for northeastern species, mostly gaining potential suitable areas of habitat (Iverson et al., 2011), and incorporated habitat, dispersal, and disturbance (Iverson et al., 2007). The vulnerability and risk for individual species under multiple climate change scenarios has also shown potential for substantial change (Duveneck et al., 2014; Zolkos et al., 2015). An extensive study was performed on central hardwood ecosystems (Brandt et al., 2041) using three different models: Climate Change Tree Atlas, LANDIS PRO, and LINKAGES. All showed significant changes in species composition. Of these, LANDIS PRO was the most similar to ED, but its domain was limited to Missouri.

This study has made important advances in using a mechanistic ecosystem model to project future change in vegetation in response to climate change over large domains. In addition to an assessment of transient responses, future work should

prioritize the inclusion of additional relevant processes, and assessment of additional climate scenarios. Boreal forests are vulnerable to climate warming which can change the fire regimes that control dominant PFT (Grace, 2002; Kasischke et al., 2010; McGuire et al., 2010). Climate change induced disturbance rate changes can alter succession (Denslow, 1980; Medvigy & Moorcroft, 2012) as these changes both impede and accelerate migration (Chapin et al., 2010). Permafrost warming alters the terrestrial carbon balance (Beck et al., 2011; Ciais et al., 2010; Turetsky et al., 2010) which adds another estimate to the net carbon storage change. Nitrogen limitation may also alter species composition (Dietze et al., 2011; Fisher et al., 2010). Future studies should incorporate these processes while also utilizing additional climate change scenarios, increasing remote sensing data use for validation, and expanding the number of PFTs for interspecies reaction to climate change. Additional climate change scenarios should be evaluated. The NARCCAP is producing numerous future climatologies from a set of regional climate models (RCMs) driven by a set of atmosphere-ocean general circulation models (AOGCMs). These can be used as inputs to models for a sensitivity analysis on transient predictions of carbon and vegetation redistribution from climate change over large domains.

2.6 Conclusions

This study used an advanced mechanistic, individually based, ecosystem model to predict the potential response of terrestrial ecosystems to climate change in North America. There are three major conclusions: (1) There are large potential changes to the distribution of plant functional types in response to future climate change; (2) There are large potential changes to the distribution of terrestrial carbon stocks in response to future climate change. These changes are largest at the grid scale, and tend to compensate at the domain scale; (3) The large potential changes warrant additional future studies on the transient response of ecosystems to climate change, and the sensitivity to alternative climate scenarios.

Chapter 3: A Pseudo-spatial Method for Predicting Future Continental Scale Plant Migration and Carbon in Response to Climate Change

3.1 Abstract

The distribution and carbon balance of ecosystems are strongly influenced by climate. With projections of climate change, it is important to understand how terrestrial vegetation will redistribute. Numerous previous studies have developed methods to estimate the potential equilibrium response to future climate change over large domains, however the transient response has proven more difficult. Plant migration ultimately depends on local plant responses and spatially explicit dispersal, but the large domain of interest presents a computationally prohibitive challenge. Here, we present a new method for projecting future continental scale plant migration and carbon redistribution. The essence of the method is a theoretical approach for estimating fine scale dispersal in a large domain pseudo-spatial modeling framework. First, we compared explicit migration to a pseudo-spatial stochastic migration simulator and derived the functional form of the equation for the stochastic simulator, then we implemented the equation in an idealized simulator, and finally we implemented in the advanced mechanistic, individual based, Ecosystem Demography (ED) model. We first present an intuitive theoretical equation for pseudo-spatial migration, the implementation in the simple simulator suggests the method produces reasonable migration rates in an idealized environment, and the initial ED results

demonstrates the method can be incorporated into most advanced models. This method provides a new way to bridge the required local scales of plant migration to larger domains of interest in a computationally efficient way and can be used in realistic future scenarios for the transient response.

3.2 Introduction

Ecosystems are strongly influenced by climate and this relationship is used to produce climate-ecosystem classification schemes. (Box, 1996; Brovkin et al., 1997; Emanuel et al., 1985; Holdrige, 1947.; Köppen, 1900; Thornthwaite, 1931; 1948). Paleoclimatology records obtained from pollen studies show that ecosystem reorganization is an anticipated consequence of climate change (Davis, 1969; Davis & Botkin, 1985; Firbas & Losert, 1949). Climate is expected to change at its greatest rate in the next century from anthropogenic forcing (Houghton & Woodwell, 1989; Vitousek, 1997) and how terrestrial ecosystems respond to the changing climate has important carbon consequences as forests contain roughly 80% of above ground carbon and sequester approximately 30% of annual fossil fuel carbon emissions (Bonan, 2008; Goetz & Dubayah, 2011; Goulden et al., 1996). With rapid climate change, rapid tree migration rates must also occur or species face extinction that can alter the expected equilibrium terrestrial carbon balance (Neilson et al., 2005).

The equilibrium response is simulated with empirical climate-ecosystem relationships or dynamic global vegetation models (DGVMs) (Brovkin et al., 1997; I. C. Prentice et al., 1992; TianGang et al., 2012) and shows relatively small net changes in carbon balance. However, this is the product of much larger underlying

grid changes in species and carbon distribution, which supports additional research of the transient response (Schaphoff et al., 2006; Solomon & Kirilenko, 1997). The transient response requires simulation with mechanistic models that account for species competition, landscape characteristics, dispersal properties, and disturbance rates (Bailey, 1983; Denslow, 1980; Hurtt & Pacala, 1995; Küchler, 1973; Plotnick & Gardner, 2002). The computational requirements of simulating these interactions often limits the domain size to the sub-continent scale (J. S. Clark et al., 2011b; Lischke et al., 2006; Menney et al., 2007).

The transient response at larger domains is currently simulated with either a top-down approach (D. B. Clark et al., 2011a) or with forest gap models (Duveneck et al., 2014; Goldblum & Rigg, 2005; Iverson et al., 2007; 2004; Peñuelas et al., 2007; Rehfeldt et al., 2006; Svenning & Skov, 2004; Sykes & Prentice, 1995). The top-down approach, used in models like JULES (D. B. Clark et al., 2011a), leaves a portion of its seed bank in every grid cell, with no grid cell interaction, and tracks species richness of a grid cell as climate changes but does not explicitly simulate migration. For explicit migration simulations, individual based, mechanistic forest gap models are used. TREEMIG (Lischke et al., 2006) is one of the more advanced forest gap models, but is limited to the subcontinent-scale from computational requirements of simulating at tree gap size. LANDIS PRO is a spatially and temporally dynamic process model that has been used to simulate migration (Brandt et al., 2014), but it too is limited to the subcontinent scale. For simulation of larger domains a representative forest can be used for scaling (Sato et al., 2007). SEIB-DGVM (Sato et al., 2007; Sato & Ise, 2012) use a 30m x 30m representative forest in

each 0.5 x 0.5 degree grid cell for Africa to simulate migration, but only at the unlimited versus no migration level.

In between these two methods is pseudo-spatial, or implicitly spatial, modeling. These are models that are non-spatial but driven with spatially structured data (Urban, 2005). For continental scale simulations of plant migration, the Ecosystem Demography (ED) model (Hurtt et al., 1998; Moorcroft et al., 2001) offers a potential way to simulate the transient response of plant migration. ED has sub-models of plant growth, mortality, phenology, biodiversity, disturbance, hydrology, and biogeochemistry that other forest gap models use, and are necessary, to simulate migration. However, ED uses a size and age-structured approximation for the first moment of the stochastic (gap) ecosystem model. Thus, the model is pseudo-spatial which decreases computation time and allows for large domain, individually based, simulations.

The question then becomes: How do you represent a spatially explicit process in a pseudo-spatial framework? To address this we examined the behavior of explicit migration versus stochastic pseudo-spatial migration and developed a theoretical function to represent the stochastic process of pseudo-spatial migration, applied the function to an idealized simulator and validated it against an explicit simulator, and initialized the ED model with our derived pseudo-spatial migration function. Specifically, this study used the (1) stochastic process of pseudo-spatial migration and (2) developed an intuitive theoretical function for pseudo-spatial migration, (3) used an idealized simulator and validated that the pseudo-spatial migration rates were reasonable, and (4) implemented the function in the advanced mechanistic ED model.

3.3 Methods

Dispersal is a fine scale process that is approached by laying a grid over a forested area. To represent the scale of this process, the grid cell size is typically that of a large canopy tree (~15m) and the fate of individuals is determined by stochastic processes representing competition for water, light, and nutrients (Pacala & Hurtt, 1995; Wright, 2002). Large domain simulations are computational prohibitive with grid cells at this scale. A way to bridge the required local scales of forest dynamics to a large domain of interest in a computationally efficient way is to scale a model to be pseudo-spatial. Pseudo-spatial simulation works by laying a larger grid over the forested area (Figure 3.1) and deriving partial differential equations that reproduce the ensemble average of the equations that govern the stochastic gap model (Hurtt et al., 1998; Moorcroft et al., 2001). Rather than simulating the stochastic processes at what is now the sub-grid, or explicit gap model scale, the individuals are grouped with a size and age-structured approximation. Thus, the total number of individuals within the larger grid cell is similar to the number of individuals the stochastic simulator would produce if the sub-grid were aggregated to the larger grid cell size, but the model goes from being spatially explicit to pseudo-spatial by grouping similar individuals. This greatly reduces the computational intensity for large domain simulations, but at the cost of explicit location, which introduces difficulties in simulating between grid cell interactions. Therefore, to simulate pseudo-spatial dispersal between grid cells we (1) compared explicit migration to pseudo-spatial stochastic migration and (2) derived a theoretical representation of our findings, (3) built an idealized simulator to validate theoretical pseudo-spatial migration rates, (4)

inserted the simulator equation into the ED model and verified that the results in a non-idealized environment were reasonable based on our understanding of the soil and climate gradients at our test sites.

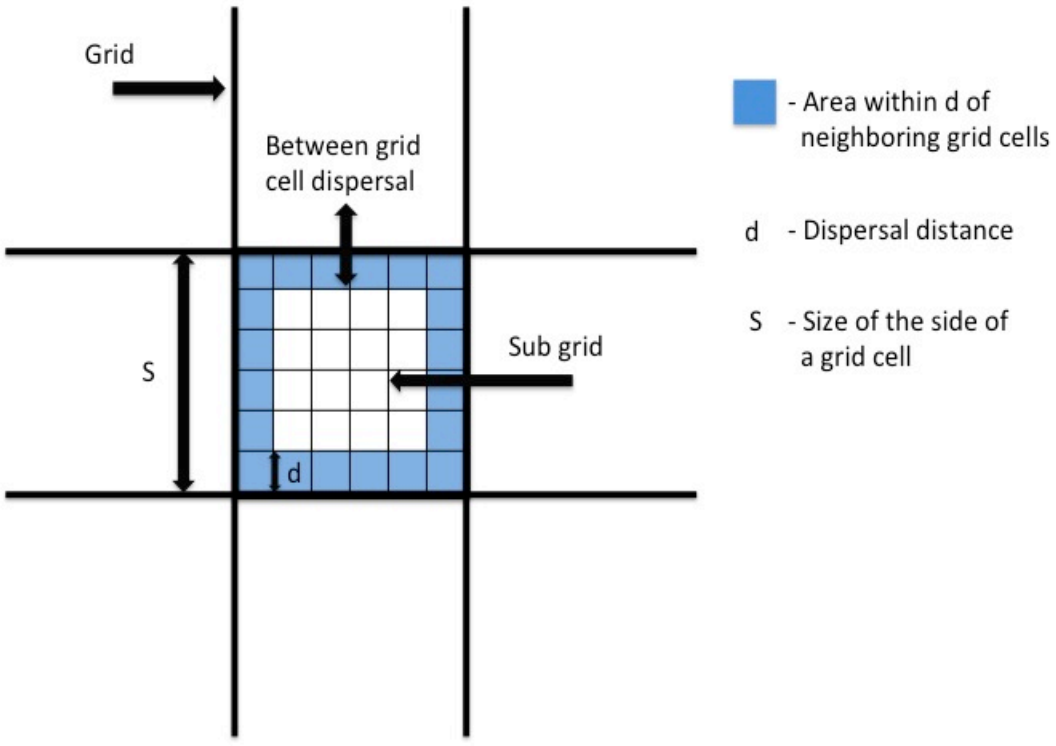

Figure 3.1. To get between grid cell dispersal pseudo-spatially (grid scale) the individuals in the spatially explicit (sub-grid) gap model are grouped by size and age-structured. Relationships between dispersal distance (d) and the size of the grid (S) are used to determine the proportion of seeds that disperse between cells.

3.3.1 Explicit vs. Pseudo-spatial Migration

Explicit migration was compared to pseudo-spatial migration rates by using a simple simulator. The simulator represented an idealized environment that had a sub-grid (explicit migration) and larger grid (pseudo-spatial). The sub-grid size of a side was set equal to the dispersal distance (d) and the grid cell size of a side (S) was set to

a multiple of the dispersal distance. For simplicity in validating, the dispersal strategy was set to be in four directions, NSEW. The center of the sub-grid (one sub-grid cell) within a grid cell was occupied and dispersal occurred at each time step. With the sub-grid size set to the dispersal distance that meant at the sub-grid level, if a cell was occupied during a time step its four neighbors became occupied from dispersal. This produced a diamond pattern of spread at the sub-grid scale (Figure 3.2). For pseudo-spatial migration, if a grid cell was occupied the relationship between d and S was used to determine the probability of dispersal to an adjacent grid cell. A coin flip based on the relationship between site size and dispersal distance used this probability to determine if dispersal to an adjacent cell occurred. After a number of simulation years, the sub-grid was aggregated to the grid size and used as a control to determine the number and location of sites the pseudo-spatial simulator should have occupied. As the pseudo-spatial simulator is stochastic, a single run is not expected to match the control case so a large number of runs averaged together were needed to replicate the explicit dispersal pattern.

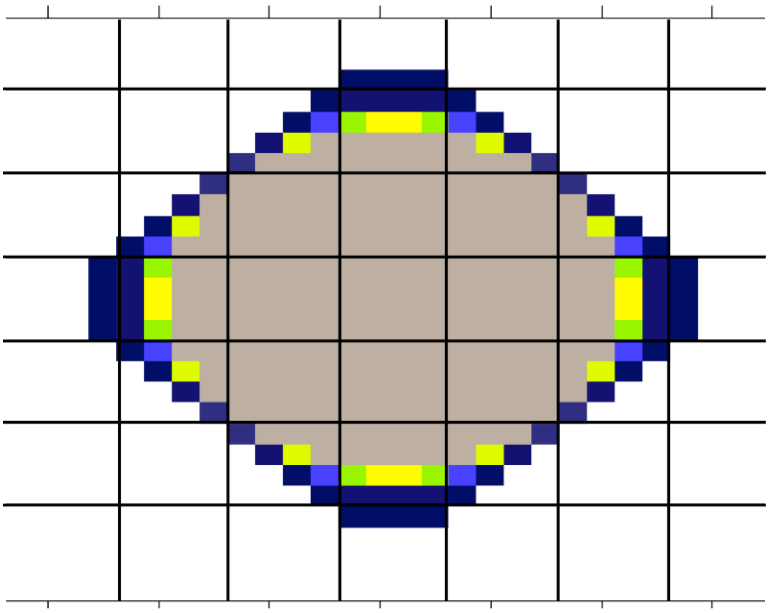

Figure 3.2. The subgrid cell scale used in the explicit simulator with the grid scale it gets aggregated to overlaying it.

3.3.2 Equation Development

The mean of a large ensemble of runs of the stochastic pseudo-spatial simulator matched the explicit result but defeated the purpose of using a pseudo-spatial framework to simulate migration as it also is not computational efficient. Therefore, we developed a theoretical representation of the probabilistic pseudo-spatial migration. We derived the fraction of dispersal that would occur at each time step rather than the integer approach of dispersal or no dispersal.

Between grid cell dispersal depends on the relationship between dispersal distance (d) and the linear side of a grid cell (S) previously discussed, as well as the number of seeds produced by individuals $N_i(t)$ of a species (i) in a grid cell, and the fraction of the grid cell they exist on $x(t)$. Thus, the proportion of seeds (P) that disperse to adjacent grid cells has the functional form:

$$P = f(x(t), N_i(t), \mathrm{d}, \mathrm{s}) \quad (1)$$

The final form of the theoretical equation was derived by assuming (1) a uniform dispersal kernel, (2) grid cells were square in size, and (3) d << s so dispersal only occurred to adjacent cells.

Dispersal kernel shapes influences migration rates, specifically with cases of apparent rapid plant migration supported by paleoclimatology research (J. S. Clark et al., 1998; J. S. Clark, Lewis, & Horvath, 2001; Davis, 2001; Davis & Botkin, 1985; Moorcroft, Pacala, & Lewis, 2006; Renton et al., 2013). Though previous research has focused on the sensitivity of exponentially versus leptokurtic bound dispersal kernels in regards to rapid plant migration (J. S. Clark et al., 1998; Moorcroft et al., 2006; Renton et al., 2013), we went simpler and made the dispersal kernel uniform. A uniform dispersal kernel aided validation of the pseudo-spatial migration rates. A uniform dispersal kernel meant that for one-dimensional dispersal on average ½ the seeds produced within the dispersal distance of the edge of a cell go off site. This rate varies when two-dimensional dispersal is implemented but the uniform kernel aided in validation.

Two-dimensional dispersal assumed that grid cell size was square to relate dispersal distance (d) to linear grid cell side (S) equally on all sides, and that dispersal occurred in four directions, NSEW. The area of the grid cell that is within dispersal distance (d) of the edge is algebraically represented as (Figure 3.1):

$$4(\mathrm{d} * \mathrm{s} - \mathrm{d}^2) \quad (2)$$

This is the area within the site that can disperse. We then accounted for corners dispersing in two directions, as per our chosen dispersal strategy, and divided by the total area of the site to get the fraction of the grid cell area that can disperse.

$$4\mathrm{d}/_{s} \tag{3}$$

The proportion of seeds that go off site then has the form:

$$P = \frac{2\mathrm{d}}{\mathrm{s}} * x(t) * N(t) \tag{4}$$

when the factor of ½ from the uniform dispersal kernel has been applied.

3.3.3 Implementation in Ideal Simulator

The simulator was then updated to represent the theoretical function rather than the stochastic process. The idealized conditions remained, with growth at each time step, but now the user specified d, S, and initial *x(t)* and *N(t)*. For the explicit component, *N* sub-grid cells at the center of the domain were initialized with one individual, and for the pseudo-spatial component one grid cell with *N* individuals was initialized to represent the difference between spatially explicit and pseudo-spatial. The starting number of individuals was chosen to represent 25% of the total number of individuals a grid cell could contain. Both versions of the simulator were then iterated through time where each individual, *N,* produced four seeds that dispersed in a NSEW direction. An individual in the explicit component therefore gave and received ½ of a seed to its four neighbors, growing by that amount where an

individual was already present and establishing in a new grid cell if not already present. For the pseudo-spatial component, equation 4 was used to calculate the total number of individuals that disperse, and then based on our chosen dispersal strategy of NSEW, ¼ of that amount moved to each adjacent grid cell. The pseudo-spatial equation meant that some fraction of seeds, however small but non- zero, would disperse to adjacent cells at every time step. To correct for this, a minimum threshold for movement was established and set to 5% of the total number of individuals a grid cell can contain. If the minimum threshold was not reached the fraction of individuals determined to disperse was stored in a seed bank, which was continuously added to during each time step, until the threshold was exceeded and then dispersal occurred. For each case, when a grid cell reached or exceeded 100% capacity, no new individuals were allowed to establish on that site. To compare explicit rates of migration to the pseudo-spatial rates, the individuals in the explicit sub-grid were aggregated to the pseudo-spatial grid size.

3.3.4 Application in ED

The scaling mechanism of ED has each grid cell comprised of a number of patches, representing the age since last disturbance, and the patches contain cohorts of individuals of plant functional types (PFTs) that are similar in size. Patches and cohorts with sufficiently similar composition are merged. Reproduction is calculated monthly at the patch level and only occurs if there is a net positive carbon balance. When this is the case, the fraction going to reproduction is a fixed fraction that a survivorship probability comprised of germination and seedling survivorship is

applied to. These rates are 30% of positive net production applied to reproduction with a 5% seedling survivorship probability (for additional details see (Moorcroft et al., 2001) appendix E). Thus, ED calculates the number of individuals to reproduce per species type $N_i(t)$ and the area of the site they were reproduced on, $x(t)$, for each monthly time step.

To simulate pseudo-spatial migration in ED, two regions were chosen based on previous research (Flanagan et al., 2016) where the dominant PFT under current climate condition was primarily one of the two PFTs used in North America (Figure 3.2). Evergreens test range was 53 to 63^0 N and -124 to -114^0 W, and deciduous test range was 40 to 50^0 N and -100 to -90^0 W. Only the central grid cell in each test range was initialized to replicate the simulators initial condition. Both test ranges include some grid cell sites with water to verify dispersal only spreads to available habitat. The rate of migration to adjacent cells for each species was examined. ED has a built in termination function where if a cohort falls below 5% cover it is removed, so the threshold for movement to an adjacent grid cell was set to this limit. If the number of individuals determined to disperse into an adjacent grid cell did not exceed the threshold, the individuals were again stored in a seed bank and continued to accumulate at each time step until the threshold was met and then dispersal occurred. The range of new cells colonized was evaluated by relating dispersal distance to the size of a side of a grid cell and compared to the expected distance covered by explicit dispersal.

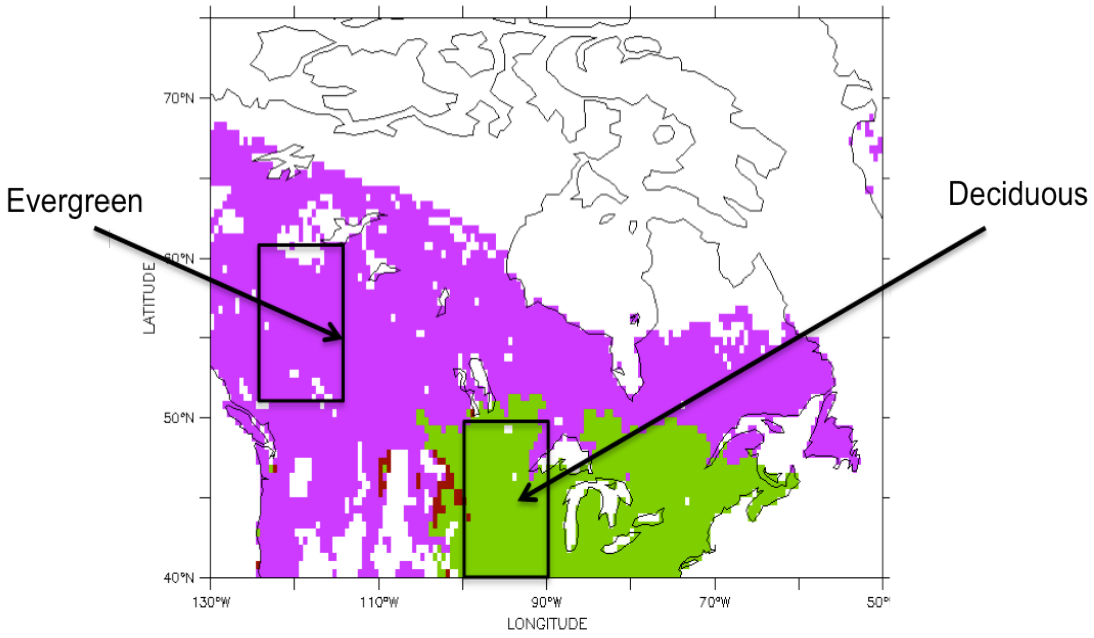

Figure 3.3. Regions used to simulate pseudo-spatial migration for each PFT.

3.4 Results

3.4.1 Simulator

The pseudo-spatial simulator was run stochastically and the probability of dispersal calcualted from the relationship between dispersal distance and grid cell side length. In this case, between grid cell dispersal occurred as a "random walk" with random numbers predicting if there was dispersal to an adjacent grid cell and in what direction based on the probability. To approach the spatially explicit simulators number of grid cells colonized with the desired spatial distribution a large number of runs of the pseudo-spatial simulated needed to be averaged together (Table 3.1). The converstion from this probability based approach to our theoretical function eliminated this need.

	# of runs	2		10		100		500	
Yr	Exp	Pseudo Avg	Abs Error %	Pseudo Avg	Abs Error %	Pseudo Avg	Abs Error %	Pseudo Avg	Abs Error %
6	5	6.5	30	4.85	-3.02	5.15	2.92	5.06	1.12
10	13	15.5	19.23	11.33	-12.82	12.44	-4.34	12.72	-2.14
14	25	24	-4	23.72	-5.11	23.75	-4.99	24.08	-3.66
18	41	37	-9.75	40.73	-0.64	39.51	-3.634	40.26	-1.80
22	61	55	-9.83	63.10	3.44	60.51	-0.80	61.80	1.30

Table 3.1. The number of grid cells that would be colonized by a given year (Exp), the average number of sites the pseudo-spatial simulator has colonized (Pseudo Avg) and the absolute error this represents. Error is reduced as the numbers of simulations averaged together increases.

Conversion to the theoretical representation of pseudo-spatial migration matched the rate of spread of the spatially explicit simulator. The rate of spread to additional grid cells is similar for the explicit and pseudo-spatial simulator when compared at the grid cell scale (figure 3.4), but varies in the spatial distribution of individuals from sub-grid cell scale properties of the explicit simulator and the use of a threshold (figure 3.2).

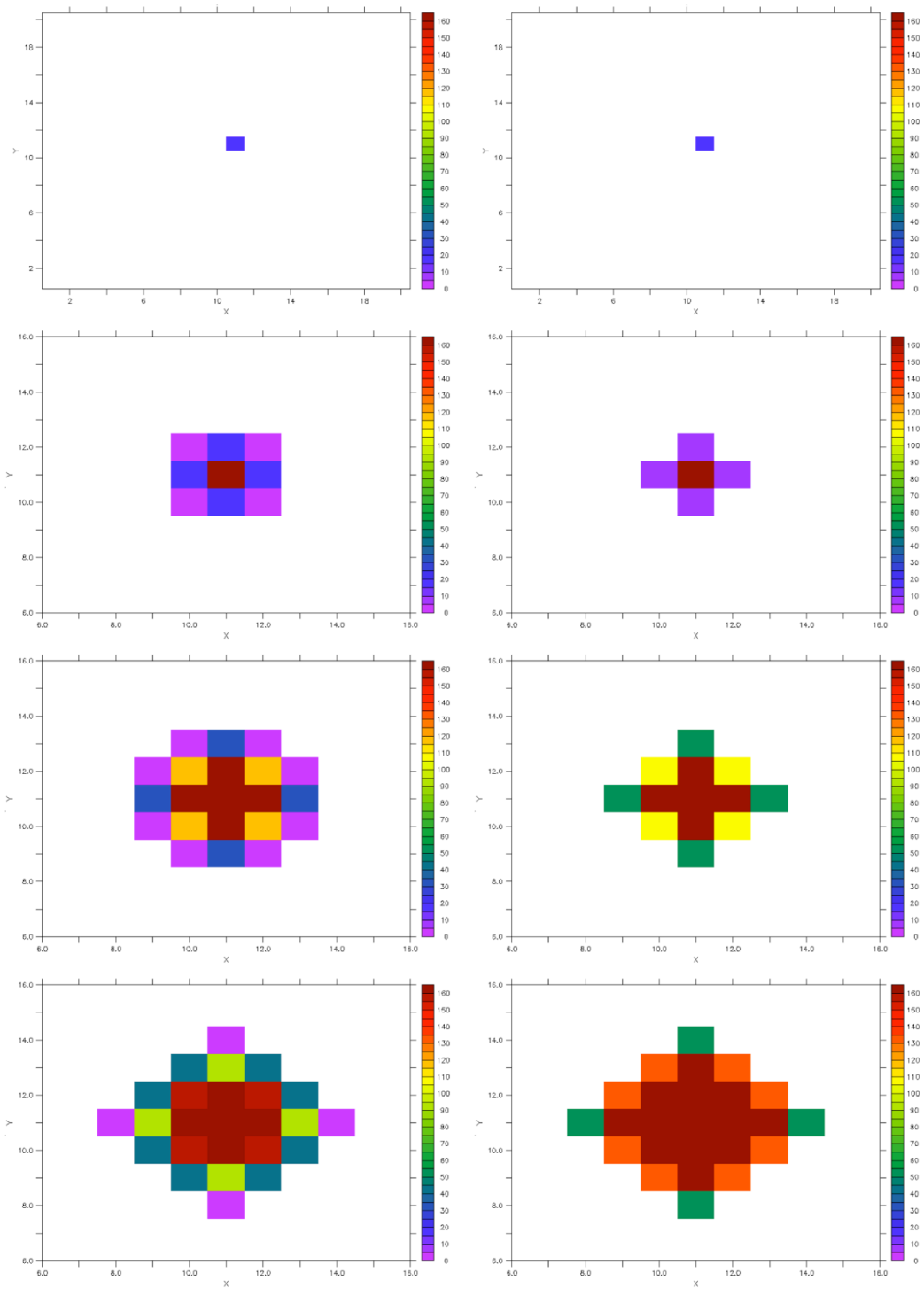

Figure 3.4. The spatial extent and number of individuals that the explicit simulator predicts when aggrageted to the grid cell scale (left) and pseudo-spatial simulator predicts (right). Slight distoration can occur depending on the time step the explicit simulator is aggregated to the pseudo-spatial scale but the general trend is observed.

Though the total number of individuals were conserved, the use of a threshold with a seed bank, and our chosen dispersal strategy, altered the spatial distribution of individuals. The NSEW strategy of dispersal increases the number of individuals on the horizontal and vertical lines in the pseudo spatial simulation (maroon on the right side of Figure 3.4). The use of a threshold with a seed bank delays establishment between these lines (green on the left in Figure 3.4). The size of the threshold, initial conditions, and time step observed alters the final pattern but the migration extent remains similar.

3.4.2 ED Model

The theoretical equation, validated with an idealized simulator, was then implemented in ED for the two North American PFTs in a domain they dominate and verified for reasonable rates (Figure 3.5). As with the simulator, the central grid cell in each test range was initiated and the rate of spread in real environmental conditions examined. Though there are a wide range of potential dispersal rates, the dispersal distance chosen was 1km to match the maximum literature rate from previous studies (Sato & Ise, 2012) and the grid cell side length was 50km to approximately match the half degree climate data used to run the model (Flanagan et al., 2016).

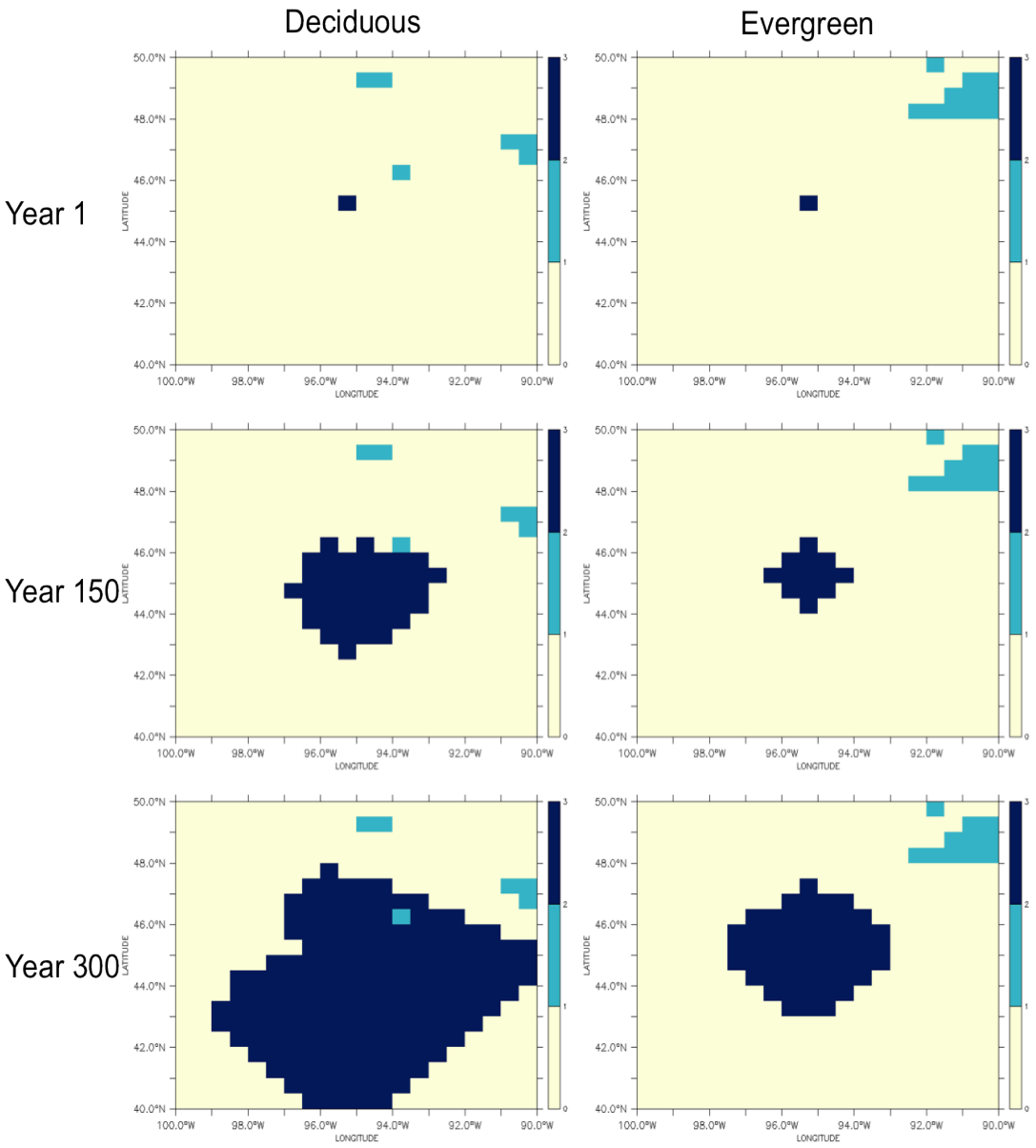

Figure 3.5. Migration (dark) of deciduous (left) and evergreen (right) PFTs into unoccupied habitat (light) and water (blue) at time steps of 150 years when migration only occurred if newly occupied grid cells would have 5% tree cover.

Times steps of 150 and 300 years were chosen because they represented spread rates of 3 and 6 grid cells respectively, in each NSEW direction, if a spatially explicit model without soil and climate gradients were used with our chosen dispersal

distance and grid cell size. We moved from an idealized environment to one with soil and climate gradients so deviations were expected. Evergreen spread in the expected diamond pattern but slightly slower than the explicit rate of 1km per year, while deciduous rapidly spread to the SE. The environmental conditions produced slower growing forests in the north causing slower migration for the evergreen PFT, and previous work showed the SE end of or deciduous test area to be high biomass deciduous forest, so accelerated growth lead to accelerated migration.

3.5 Discussion

This study compared explicit dispersal to stochastic pseudo-spatial dispersal and developed a theoretical function to represent pseudo-spatial dispersal, validated the function with an idealized simple simulator in a uniform landscape, and implemented the function in an advanced mechanistic, pseudo-spatial, ecosystem model. Future studies will be able to use this method to examine the transient response at continental to global scales, rather than the local scales most gap models are limited to from computational requirements.

The theoretical function is derived from the mean ensemble of the stochastic pseudo-spatial simulator. Rather than determine if dispersal does or does not occur, the function determines the proportion of seeds that should disperse based on dispersal distance, site size, area occupied, and seeds produced. Therefore, as long as the value is non-zero rapid spread across the landscape, however small, is expected. To prevent rapid spread across the landscape a threshold for movement must be used in combination with a seed bank to conserve seeds that do not meet the threshold, and

hence do not disperse to adjacent grid cells. These methods can distort the spatial distribution of individuals (Figure 3.4) but predict the general pattern of spread to new grid cells. We set the threshold to ~5% tree cover in newly colonized cells because although rapid dispersal across the landscape was not desired, neither was a potentially large time-lag to establishment that would influence transient response evaluation. The threshold for movement to prevent instantaneous dispersal was low enough to not change establishment time by more than a few years. Comparison of the rate of migration in both the explicit simulator and theoretical pseudo-spatial simulator demonstrated this is a viable method for large domain migration simulation. The threshold can be adjusted depending on simulation requirements.

Application of the equation in the ED model with dispersal distance set to the maximum literature value of 1 km/year (Sato & Ise, 2012; Solomon & Kirilenko, 1997) and a grid cell size of ~50km predicted movement to adjacent grid cells in a environment with soil and climate gradients. The test areas for the model (Figure 3.3) were chosen because they consisted of a dominant PFT, but also because our previous research showed them to be transition zones for PFTs on their northern extents for the equilibrium response to climate change (Flanagan et al., 2016). With the threshold, deciduous disperses north at ~1 grid cell per 50 year time step, similar to what spatially explicit migration would predict. For deciduous, the SE is an area where they dominate and reproduce quickly (larger $N(t)$), so rapid dispersal occurs in this direction but would not change the dominant PFT or carbon redistribution from climate change associated with transient response simulations. For evergreen their rate is slightly slower but expected from the shorter growing season at this higher

latitude. The threshold can be altered dependent on the needs of the scenario, but these are reasonable results for the environmental gradients at the test areas.

This study focused on the development of a method to simulate the transient response of vegetation over large domains. Mechanistic, individually based ecosystem models are necessary to capture the local climate and soil properties, as well as competition for resources and establishment, that influence migration rates (Bachelet et al., 2001; Neilson et al., 2005; I. C. Prentice et al., 1992). The computational requirements to simulate these process often lends itself to research at the landscape scale (Brandt et al., 2014; Iverson et al., 2007; 2004; Zolkos et al., 2015). The ED model uses a size and age-structured approximation for the first moment of the forest gap ecosystem model so it decreases computation time and allows for large domain simulation, but presents challenges when simulating spatial processes in its pseudo-spatial environment. Here we developed and validated a method to represent migration pseudo-spatially in ED

For future research, we plan to alter the disturbance rates, dispersal strategies, and migration rates in ED to determine migrations influence on the carbon balance and dominant PFT distribution in northern North America. Now that ED has been modified to include a pseudo-spatial function for migration, and our research on the equilibrium response showed large underlying grid changes, it is the ideal model for large domain simulation of the transient response of vegetation to climate change. Transient dynamics of the forest community such as landscape heterogeneity and disturbance regimes influence migration rates (Sykes& Prentice, 1995; C. D. Thomas et al., 2004). Disturbance and landuse history are closely linked and have been

shown to both accelerate and impede migration rates (Dale et al., 2001; Midgley et al., 2007; Theoharides & Dukes, 2007). Disturbance rates control the probability of new species establishment as some disturbance is needed for new species to enter an ecosystem but too much prevents establishment (Denslow, 1980; Emanuel et al., 1985). The functionality of the model to change grid cell size and disturbance distance will allow us to account for Reid's Paradox of long distance dispersal events (J. S. Clark et al., 1998; Moorcroft et al., 2006; Raupach & Canadell, 2010). Mechanistic, individually based, forest gap models are necessary to simulate these interactions and the size and age-structure approximation of the first moment of a gap model utilized in ED will allow for large domain simulation of the transient response now that a computationally efficient method to simulate pseudo-spatially migration has been developed.

3.6 Conclusion

This study developed a theoretical equation to represent the stochastic pseudo-spatial dispersal process. Implementation of the equation in an idealized environment verified the general pattern of spatially explicit dispersal could be replicated with the intuitive theoretical equation. Application in an advanced ecosystem model produced expected results with prior knowledge of the soil and climate gradients of the test area, which opens numerous possible studies on the impact of the transient response of migration on vegetation and carbon redistribution from climate change. Fine scale characteristics such as dispersal, disturbance, and competition often limit the domain of simulations of the transient response of migration to the subcontinent scale, but the method derived in this research will allow future research to examine these in continental, and potentially larger, domains.

Chapter 4: Potential Transient Response of Terrestrial Vegetation and Carbon in Northern North America from Climate Change

4.1 Abstract

Terrestrial ecosystems are closely coupled with climate. Anthropogenic forcing has the potential to accelerate climate change, altering terrestrial vegetation and carbon distribution. Previous studies have empirically estimated both the equilibrium and transient response of terrestrial carbon to climate change at scales up to globally, but research on the transient response of vegetation to climate change is often limited to the sub-continent scale. Estimation of the transient response of vegetation requires the use of mechanistic models to predict the consequences of competition, dispersal, landscape heterogeneity, disturbance, and other factors, where it becomes computational prohibitive at scales larger than sub-continent. Pseudo-spatial models are used to reduce computational intensity, but present challenges in representing spatially explicit process, such as migration, in a pseudo-spatial framework. Here, we use an advanced mechanistic, individually based, pseudo-spatial ecosystem model that recently had a pseudo-spatial migration sub-model developed, to predict the transient response of vegetation and carbon to climate change in northern north America. The model was first run with a current climatology at half-degree resolution for 1000 years to establish current vegetation and carbon distribution. The climate was then abruptly changed to a future

climatology and run for an additional 2000 years with different combinations of dispersal rates, dispersal modes, and disturbance rates for 18 total scenarios of 36000 simulation years. The average effect that each independent variable had at the end of the simulation when compared to the predicted equilibrium response of total carbon and dominant plant functional type were: disturbance on carbon 7.49 ± 2.22%, disturbance on PFT distribution 7.81 ± 2.73%, dispersal rate on carbon 6.54 ± 3.19%, dispersal rate on PFT distribution 14.13 ± 4.75%, dispersal mode on carbon 9.04 ± 4.3%, dispersal mode on dominant PFT 3.77 ± 2.3%. Percentage of predicted equilibrium carbon ranged from 94% to 116% with a mean value of 107%, and percentage of predicted equilibrium dominant plant functional type distribution matched ranged from 60% to 86% with a mean of 74%. Other findings showed faster migration with increased disturbance, maintenance of forests at northern latitudes that are not self-sustaining without migration, and an initial increase in above ground biomass before migration occurs. This work illustrates that large domain simulations of the transient response are possible in advanced, mechanistic ecosystem models and continued research should further explore the interactions between competition, dispersal, and disturbance, particularly in regards to changes in vegetation type.

4.2 Introduction

Ecosystems are strongly influence by climate (Holdrige, 1947.; Köppen, 1900; Thornthwaite, 1931; 1948) and these relationships are used to forecast the redistribution of ecosystems from climate change. (Box, 1996; Emanuel et al., 1985). Redistribution under elevated climate change was explored by Emanuel with the use of a map of the Holdrige Life-Zone Classification under increased CO_2 and found the

largest changes occur in boreal forest zones (Emanuel et al., 1985). As forests contain ~80% of above ground carbon and sequester ~30% of annual fossil fuel emissions they have a prominent role in the carbon balance (Goodale et al., 2002; Houghton, 2005). The equilibrium change in terrestrial carbon from ecosystem redistribution is found using Dynamic Global Vegetation Models (Schaphoff et al., 2006; Solomon & Kirilenko, 1997). Schaphoff *et al.* used the LPJ-DGVM with five different climate change scenarios and found the global change in carbon storage ranged from -106 to 201 PgC by the end of the century (Schaphoff et al., 2006). Solomon and Kirilenko used multiple climate change scenarios with the BIOME 1 model and found that instantaneous redistribution versus no redistribution decreased terrestrial carbon from 7 to 34 PgC (Solomon &* Kirilenko, 1998). The magnitude and response of these findings supports research into the transient response of vegetation to climate change.

The transient response of vegetation requires the use of mechanistic models that capture plant competition, dispersal strategies, landscape characteristics, disturbance regimes, and other fine scale processes (J. S. Clark et al., 2001; Dietze et al., 2011; Medvigy & Moorcroft, 2012; Soja et al., 2007; Van Minnen et al., 2000). Long distance rapid dispersal is governed by, and sensitive to, the tail of the dispersal kernel (J. S. Clark et al., 2011b; Davis, 2001; Renton et al., 2013) and accounts for Reid's Paradox of rare long distance dispersal events (Clark et al., 1998; Bailey, 2004; Kot et al., 1996). Disturbance rates can both impede and accelerate migration (Sykes & Prentice, 1996) as some disturbance is needed for new species to enter a mature forest but too much prevents establishment (Denslow, 1980). Some species

may "win by forfeit" due to recruitment limitation (Hurtt & Pacala, 1995) that slows population and community dynamics and can enable the persistence of a species that would otherwise be out competed. Landscape heterogeneity can produce corridors that aid migration (Renton et al., 2013). These are all fine scale processes that are captured by mechanistic models and should be addressed when simulating the transient response of vegetation to climate change.

The computational time to simulate these processes often leads to studies at the local to sub-continent scale (Duveneck et al., 2014; Lischke et al., 2006; Rehfeldt et al., 2006). To simulate the transient response of migration at large scales there are two major approaches, top down and representative forest (D. B. Clark et al., 2011a; Sato et al., 2007; Sato & Ise, 2012). The top down approach, used in JULES (D. B. Clark et al., 2011a), leaves a portion of its seed bank in every grid and the dominant plant functional type can change over time but there is no between cell migration. Forest gap models such as TREEMIG (Lischke et al., 2006), LANDIS PRO (Sturtevant, et al., 2004; Wang et al., 2014), and SEIB-DGVM (Sato et al., 2007) all simulate migration but at the subcontinent scale. To move to a larger domain, a representative forest can be scaled to a larger grid size, but with the loss of some of the underlying fine scale processes (Sato et al., 2012).

Here, we used an advanced individually based mechanistic model that is pseudo-spatial, which decreased computational time to overcome the scale limitation, and predicted the transient response of vegetation and carbon to climate change in northern North America. The model contains a recently developed sub-model of pseudo-spatial migration that was used to evaluate the transient response of

vegetation and carbon from climate change. Specifically, this study predicted the impact of (1) dispersal distance, (2) dispersal mode, and (3) disturbance rate on the potential redistribution of terrestrial vegetation and carbon from climate change in northern North America.

4.3 Methods

4.3.1 Model

The Ecosystem Demography (ED) model (Hurtt et al., 1998; Moorcroft et al., 2001) is a mechanistic model that uses a size and age-structured approximation for the first moment of the spatial stochastic process of vegetation dynamics. The size and age-structured approximation means it is an individual-based model of vegetation dynamics that is pseudo-spatial instead of spatially explicit. Individuals compete mechanistically for water, nutrients, and light governed by sub-models of growth, mortality, water, phenology, biodiversity, disturbance, hydrology, and soil biogeochemistry. Plants in ED are represented by plant function types (PFTs), which group vegetation into classes dependent on physiognomy, leaf, form, photosynthetic pathway, and other characteristics (Foley et al., 1996), and are adjusted for the region of study. Following Hurtt *et al.* 2002 (Hurtt et al., 2002), trees in North America are represented by two dominant types, cold deciduous and evergreen, with the modifications made by Flanagan *et al.* 2016 (Flanagan et al., 2016). ED has been successfully implemented in South, Central, and North America, as well as the United states. It is currently being used in NASA's Carbon monitoring System (Hurtt et al., 2015) and the NASA planned mission GEDI.

ED was run for 1000 years with current and future climate data in the domain of northern North America (40°N to 75°N and 165°W to 50°W) to establish equilibrium PFT and carbon distribution for each climate. The average year of the entire current climate data set (1901-2010) was used as the driver for current distribution, and the average of the last five years of the future climate data set (2065-2070) used for future distribution. Future anthropogenic climate change and migrations response is a concern in magnitude and pace (Loarie et al., 2009; Zolkos et al., 2015). Ecologically, climate changes faster than ecosystems redistribute. To evaluate the upper limit of this we changed climate first, followed by migration, though future studies can consider jointly.

A model experimental design evaluated the impact factors of dispersal rate, dispersal mode, and disturbance rate. Eighteen cases were considered; dispersal rates of 0.1km, 1km, and 10km; disturbance rates at the models standard 1.2%, doubled and tripled; and directed or even dispersal (Table 4.1). Directed dispersal had individuals migrate to recently disturbed areas and even dispersal was spread proportionally across a grid cell. Each scenario started with the results from the 1000 years run of the current climatology for initial biomass and PFT distribution, and was run for an additional 2000 years with the future climatology for a total of 36000 model simulation years. The transient response results were evaluated by percent total carbon and percent dominant PFT type of the equilibrium case they predicted. Dominant PFT of a grid cell was determined by applying the National Land Cover Dataset 1992 (NLCD92) (Vogelmann et al., 2001) classification for forest

composition of 75% cover of a particular type, deciduous or evergreen, otherwise the forest was classified as mixed. Sites below 25% cover are considered non-forest.

Disturbance Rate (1x, 2x, 3x)	Dispersal Distance (.1km, 1km, 10km)	Dispersal mode (even, directed)
1x	.1 km	Even
1x	.1 km	Directed
1x	1 km	Even
1x	1 km	Directed
1x	10 km	Even
1x	10 km	Directed
2x	.1 km	Even
2x	.1 km	Directed
2x	1 km	Even
2x	1 km	Directed
2x	10 km	Even
2x	10 km	Directed
3x	.1 km	Even
3x	.1 km	Directed
3x	1 km	Even
3x	1 km	Directed
3x	10 km	Even
3x	10 km	Directed

Table 4.1. The 18 scenarios used to determine the impact of migration on vegetation and carbon redistribution. Three different disturbance rates with three dispersal rates, and two dispersal modes.

4.3.2 Climate data

Two climate data sets were used. A current climate data set established contemporary carbon and PFT distribution as supported by remote sensing data (Flanagan et al., 2016), and a future climate data set for the model experimental design and equilibrium response. The current climate data set was from the Multi-

Scale Synthesis and Terrestrial Model Intercomparison Project (MsTMIP) conducted by the North America Carbon Program (NACP) (Wei et al., 1994; 2013). It is a combination of the Climate Research Unit (CRU) and National Centers for Environmental Prediction (NCEP) climatologies at 0.5 x 0.5 degree global resolution from 1901 – 2010 in a WGS84 projection at 6 hourly daily time steps. The future climate data set was from the North American Climate Change Assessment Program (NARCCAP), which produces multiple future climatologies at ~50km resolution (Mearns et al., 2009). Future climate projections are provided by coupling a set of regional climate models (RCMs) driven by a set of atmosphere-ocean general circulation models (AOGCMs) forced with the Special Report on Emission Scenarios (SRES) A2 scenario for the 21st century. The combination of the Community Climate System Model (CCSM) as the driving model and MM5I as the regional model were used and contained future climate data from 2041-2070 at 3 hourly daily time steps in a Lambert Conic Conformal projection. The NARCCAP climate data set was converted to half-degree resolution with a WGS84 projection to match the current climate data set.

4.4 Results

4.4.1 Effect of Independent Variables

Each disturbance scenario alters the predicted potential equilibrium carbon and dominant PFT distribution so three future equilibrium scenarios were run that 6 of the 18 scenarios were compared to, along with the current dominant PFT distribution that each scenario was initialized with (Figure 4.1). At the end of the

2000 year simulation the percent of predicted total carbon and dominant PFT distribution when compared to the equilibrium predictions ranged from; 94% to 116% total carbon with a mean value of 107%, and 60% to 86% dominant PFT sites matched with a mean of 74% (Table 4.2).

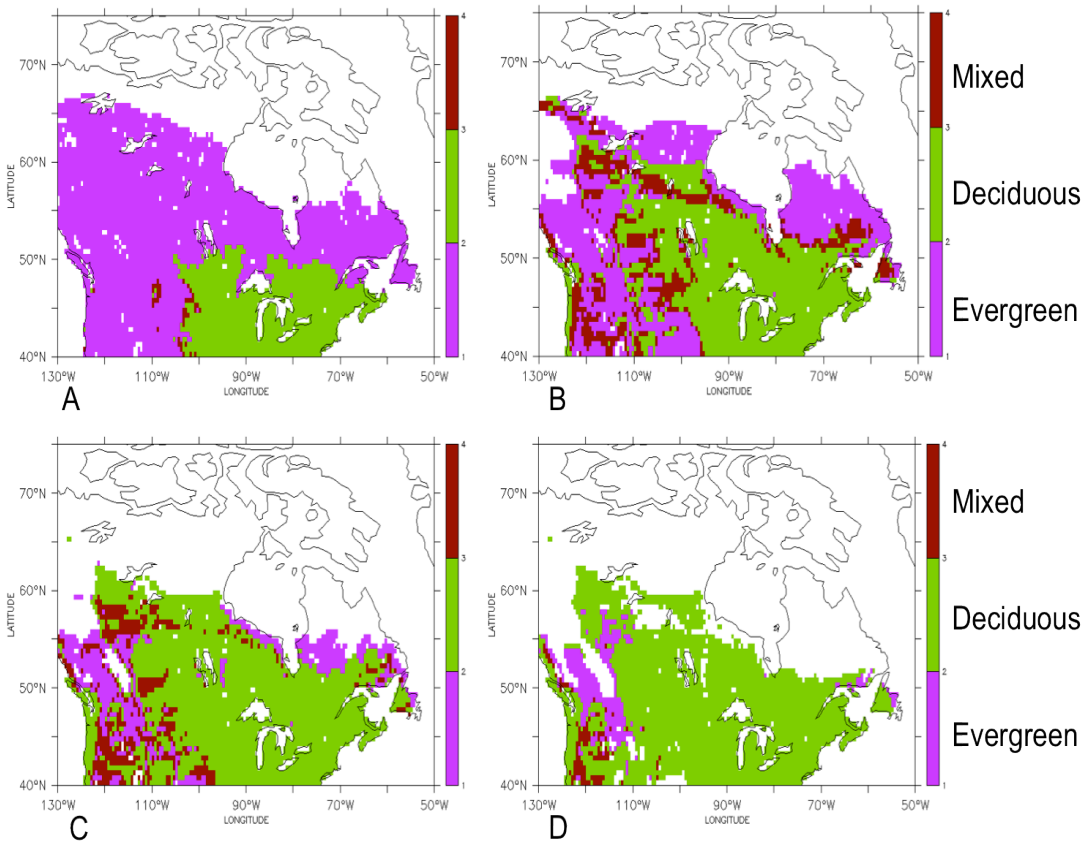

Figure 4.1. The current dominant PFT distribution (A) that each scenario started from and the predicted future equilibrium distributions of dominant PFT with the standard disturbance rate (B), and with disturbance doubled (C) and tripled (D).

Scenario	% carbon	% PFT
Direct .1km	107	68
Direct 1km	104	81
Direct 10 km	103	86
Even .1km	110	67
Even 1km	109	74
Even 10km	106	83
Direct .1km, disturbance x2	108	65
Direct 1km, disturbance x2	103	76
Direct 10 km, disturbance x2	110	80
Even .1km, disturbance x2	116	60
Even 1km, disturbance x2	113	69
Even 10km, disturbance x2	112	78
Direct .1km, disturbance x3	98	68
Direct 1km, disturbance x3	94	73
Direct 10 km, disturbance x3	106	74
Even .1km, disturbance x3	114	68
Even 1km, disturbance x3	111	75
Even 10km, disturbance x3	112	76

Table 4.2. The percentage of predicted equilibrium carbon and dominant PFT sites matched for each scenario at simulation year 2000. Different rates of disturbance were compared to different final equilibrium conditions as shown in Figure 4.1.

To isolate the magnitude of the effects, the average RMSE between the equilibrium and scenario predictions for each independent variable were calculated (Figure 4.2). The magnitudes were: disturbance on carbon 7.49 ± 2.22%, disturbance on PFT distribution 7.81 ± 2.73%, dispersal rate on carbon 6.54 ± 3.19%, dispersal rate on PFT distribution 14.13 ± 4.75%, dispersal mode on carbon 9.04 ± 4.3%, dispersal mode on dominant PFT 3.77 ± 2.3%.

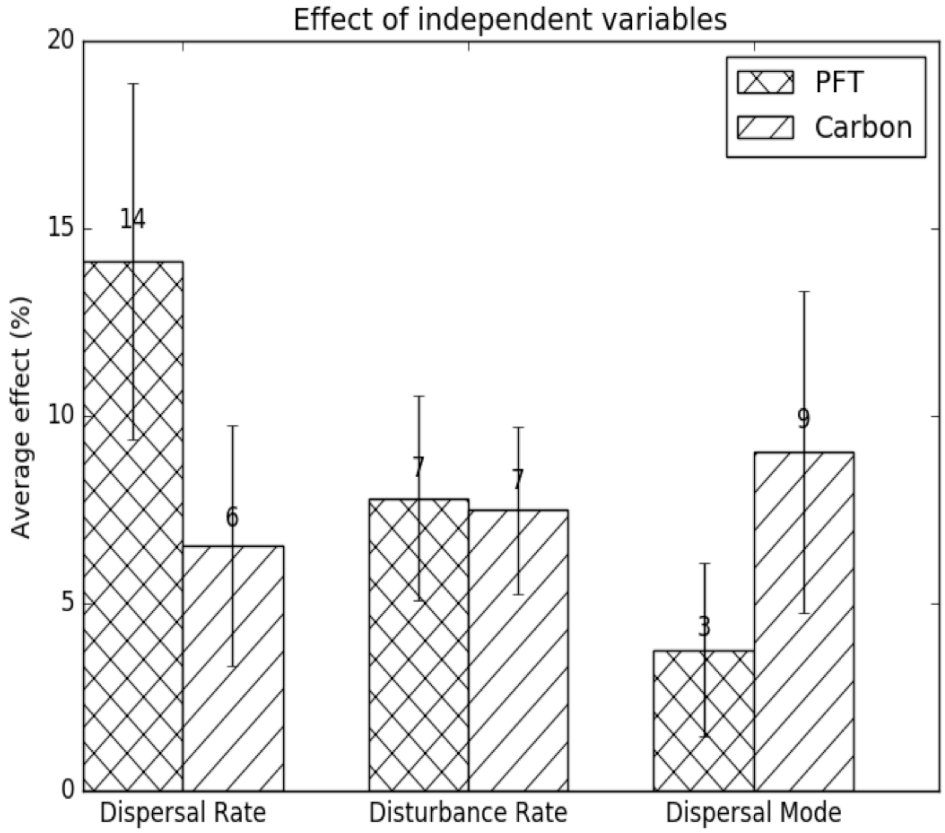

Figure 4.2. The RMSE of the average effect that each independent variable has on the percent of equilibrium carbon and dominant PFT distribution matched in the scenarios.

The dispersal mode has the largest effect on the percentage of equilibrium carbon matched, with the greatest contribution from the direct mode of tripled disturbance. The only two scenarios where the percentage of equilibrium carbon matched was less than 100 percent occurred here (Table 2). The combination of lower total over all carbon and with directed dispersal lead to an increased number of sites with biomass, but fell below the defined cutoff of 2 kg/m2 to be considered a forest (Figure 4.3). The checkerboard pattern is an artifact of being a snapshot of a single year. Directed migrates faster so it has a higher northern extent than even

dispersal, but without continuous migration intermediate sites loss their biomass so at any given yearly snapshot different sites may show very low biomass or no biomass at all.

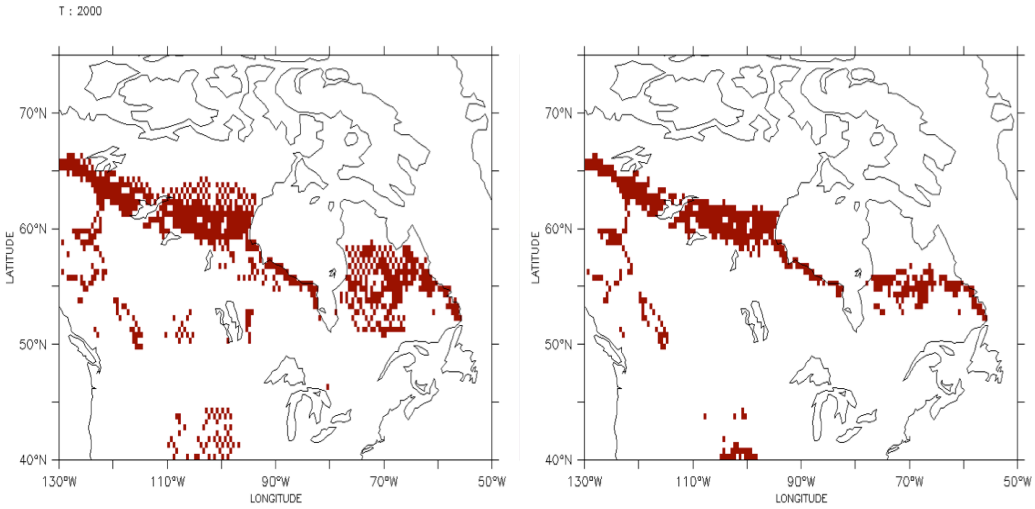

Figure 4.3. Sites that contain biomass but are not included in the carbon calculation because they fall below the threshold of forest classification for directed (left) and even (right) dispersal at 0.1km per year with a tripled disturbance rate.

Dispersal rate had the largest effect on the percentage of sites that matched the predicted equilibrium distribution of dominant PFT, with values always lower than 100%. To evaluate, we compared the 0.1km rate verses the 10km under standard disturbance for directed dispersal (Figure 4.4):

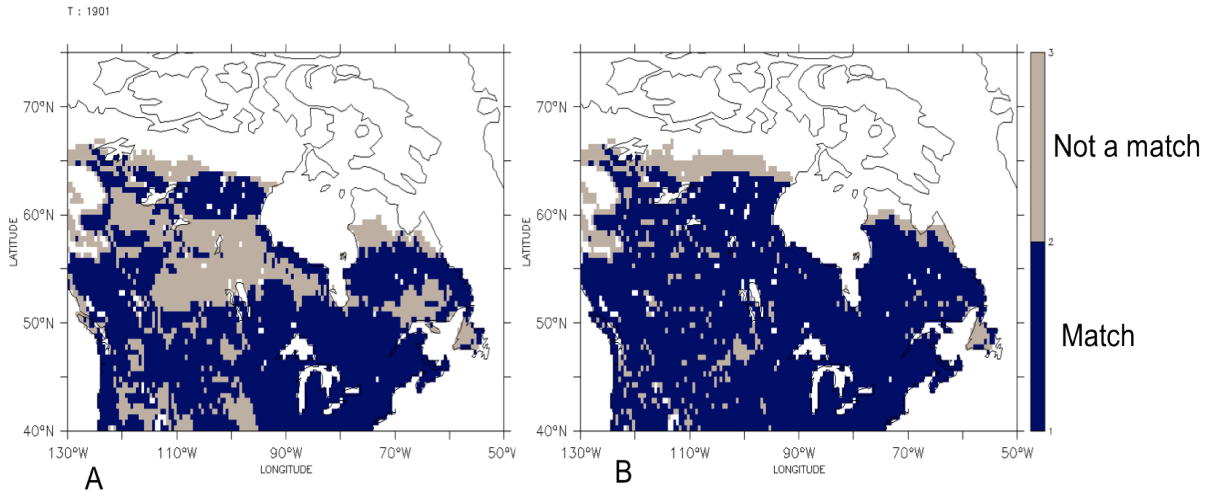

Figure 4.4. Sites that match the predicted equilibrium dominant PFT distribution for directed dispersal under standard disturbance with a dispersal rate of 0.1km (left) and 10km (right).

Directed dispersal at 0.1km matched 68% of the predicted equilibrium sites and at 10km matched 86% of the sites, but the inability to reach 100% differs for each case. Comparison to Figure 4.1 parts A and B showed that 0.1km dispersal is not a large enough dispersal rate for either evergreen or deciduous to migrate to the predicted equilibrium locations. Deciduous forests have not migrated NW into an area they were predicted to become the domain PFT (Figure 4.4A, gray in the middle) or evergreen expand to its furthest extent north (Figure 4A, gray at top). For 10km dispersal, enough simulation years had passed for the majority of the domain to match the predicted equilibrium PFT distribution (Figure 4.4B, blue), but migration actually maintains forested area further north than the equilibrium scenario predicted (Figure 4.4B, gray at top). Migration of additional individuals prevented forest collapse.

Disturbance rate had the intermediate effect on both the percentage of carbon and dominant PFT distribution matched of the predicted equilibrium response. This

is because increased disturbance decreased the time it took the deciduous PFT to migrate (Figure 4.5) and decreased the northern evergreen range when compared to Figure 1 parts C and D, but not as far south because of the additional northern forest maintenance from new individuals migrating (Figure 4.6).

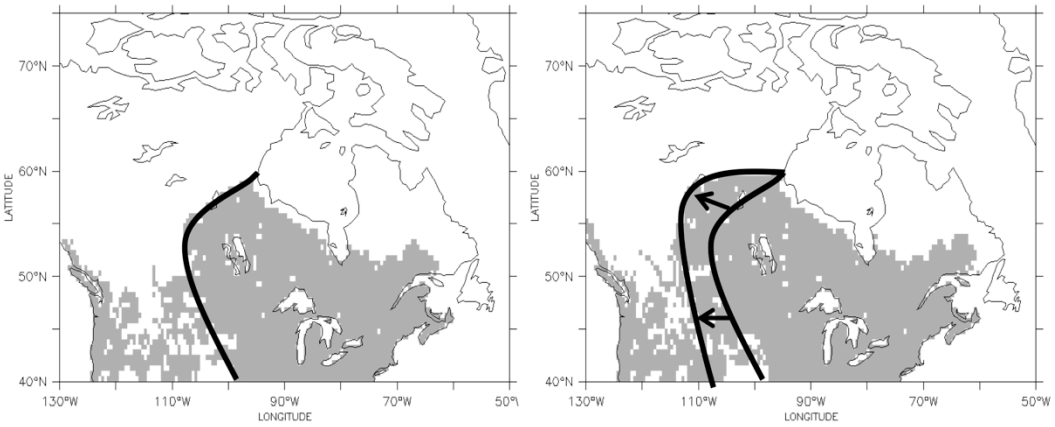

Figure 4.5. The extent that deciduous forest migrates at 1km a year with directed dispersal at the standard disturbance rate (left) and when the disturbance rate is doubled (right) with the increase in the wave front highlighted.

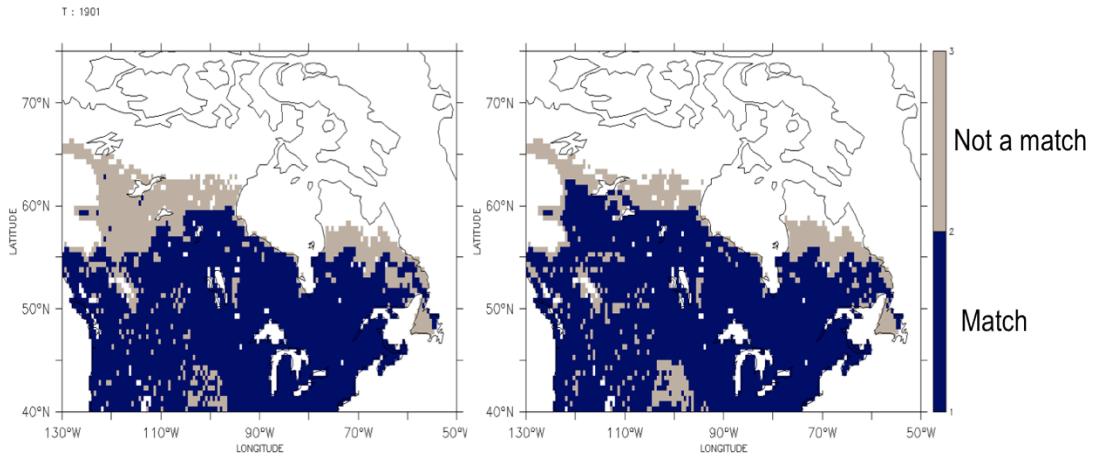

Figure 4.6. Sites that match the predicted equilibrium dominant PFT distribution under doubled disturbance for 1km (left) and 10 km (right) directed dispersal.

Directed dispersal at 1km with disturbance doubled was closer to matching total carbon than the same scenario at 10km from being an intermediate effect. Fluctuations in biomass were masked out between -2kg/m2 and 2kg/m2 and the total biomass for 1km directed migration with disturbance doubled (Figure 4.7A) had compensating high and low zones with respect to the equilibrium case, with the high zone coming from evergreen biomass that had not yet been replaced by the expected deciduous dominant PFT (Figure 4.7B). For 10 km, there is less compensation as the dominant PFTs have established and the persistence of northern forest is responsible for the increased total carbon (Figures 4.7C and 4.7D).

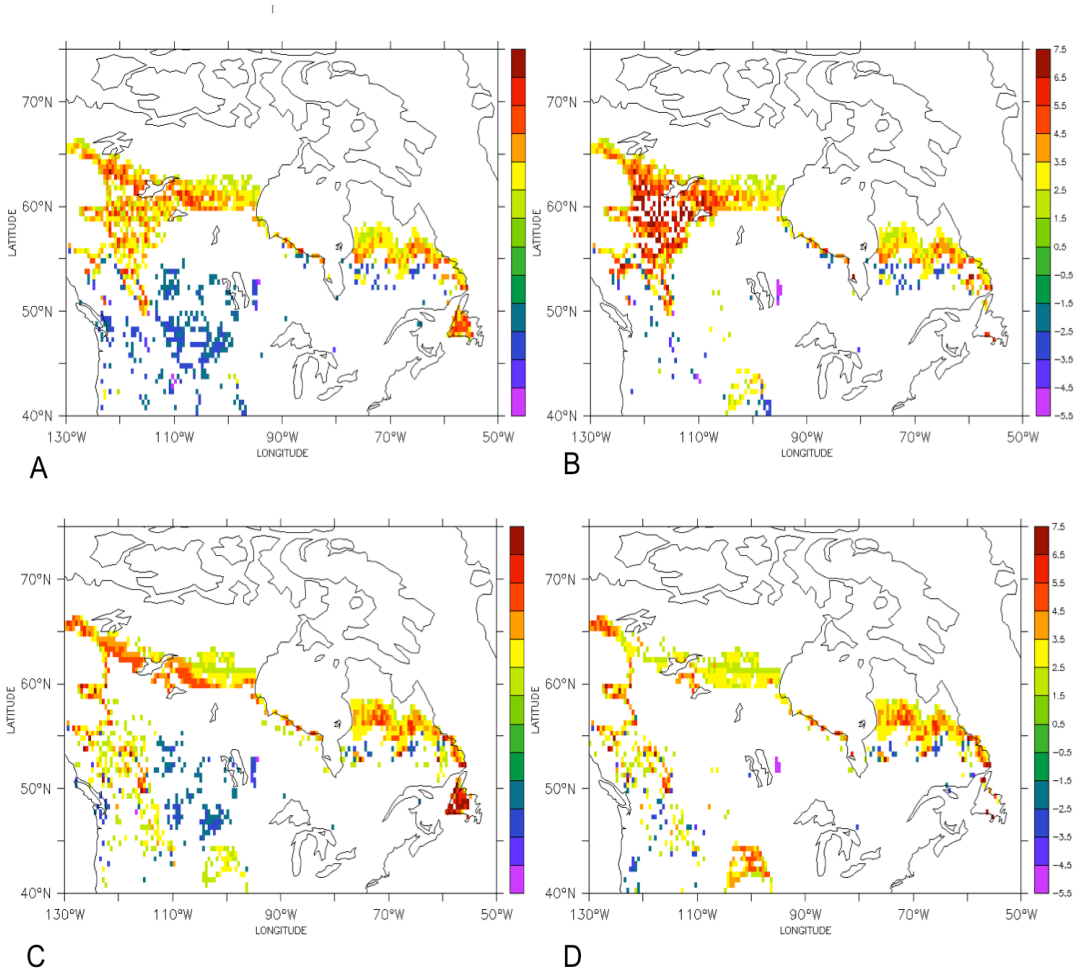

Figure 4.7. Areas where the amount of biomass is 2 kg/m2 higher or lower the predicted equilibrium value for directed dispersal with disturbance doubled for 1 km (A) and 10 km (C), and the amount that comes from evergreen (B) and (D). 1km migration, though faster with disturbance doubled, still has not finished migrating so evergreen forest persist in an area that will become deciduous dominant (B), while 10km migration has established but produces more above ground carbon than the equilibrium case as migration sustains northern and edge forests that otherwise would become non forest (D compared to 4.1C)

Plotting Table 4.2 as percent of equilibrium carbon and dominant PFT obtained by each scenario visually highlights these findings (Figure 4.8).

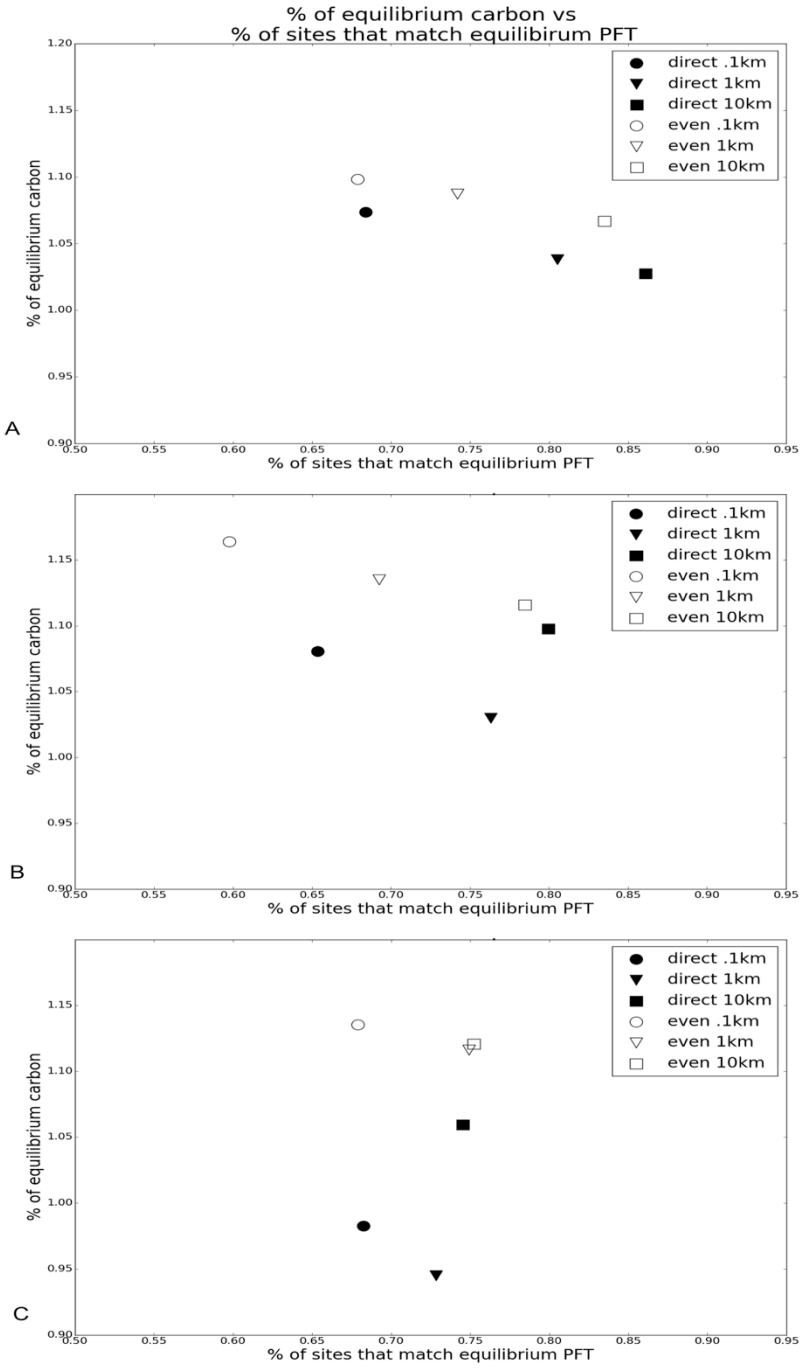

Figure 4.8. The 18 scenarios as the percentage of predicted equilibrium carbon and dominant PFT they achieved after 2000 simulation years divided into plots by standard (A) doubled (B) and tripled (C) disturbance rates.

4.4.2 Temporal Response

Total carbon and the percent that came from deciduous and evergreen PFTs were tracked with time. Each case showed the evergreen PFT increase in total carbon at the start of the simulation (Figure 4.9). This causes total carbon to overshoot the predicted equilibrium total carbon before approaching, but did not equaling, future predicted total carbon. The predicted future equilibrium deciduous dominant PFT range was only approached with dispersal set to 10km per year.

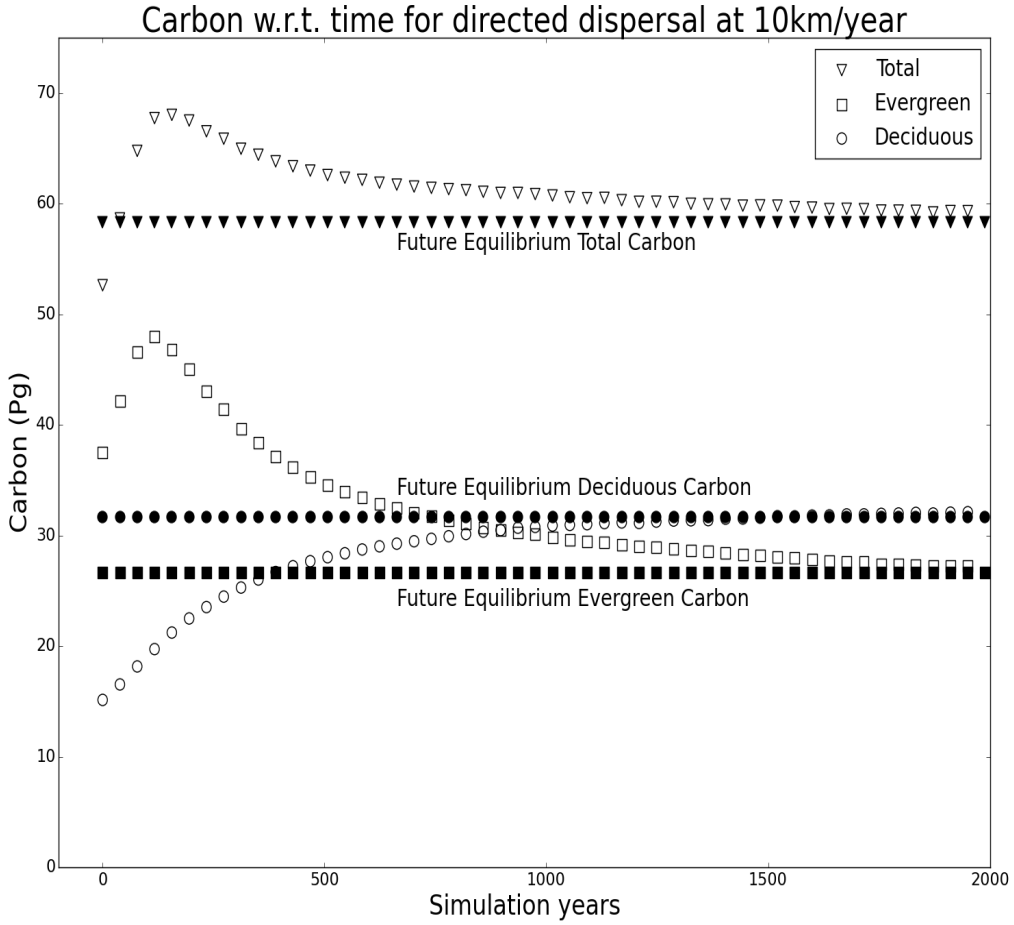

Figure 4.9. Total carbon, and the portion from deciduous and evergreen PFTs, with respect to simulation year are shown in white. Black represents predicted future equilibrium carbon.

To evaluate the upper limit of climates impact, it was changed before migration started. The dominant PFTs did not have time to redistribute. The difference of the total carbon at year 100 of the directed dispersal case with standard disturbance and the predicted equilibrium carbon showed that total carbon by site increased modestly (Figure 4.10A). The difference of evergreen total carbon at year 100 and the predicted equilibrium carbon highlighted that the lack of a change in dominant PFT is the cause (4.10B). The increase in carbon is a result of the evergreen PFT not being replaced by the deciduous PFT at this simulation year. The evergreen PFT, though not predicted to exist here in the equilibrium response, can grow 1-2kg/m^2 larger with the future climate. We also see a deficit in carbon at the northern boundary as not enough time has passed for migration to this area to occur. By simulation year 2000, the dominant PFTs have redistributed and the total carbon (4.10C) mostly matches the predicted equilibrium carbon with the exception of the northern forests, which expanded farther north than the predicted equilibrium future scenario (4.10D).

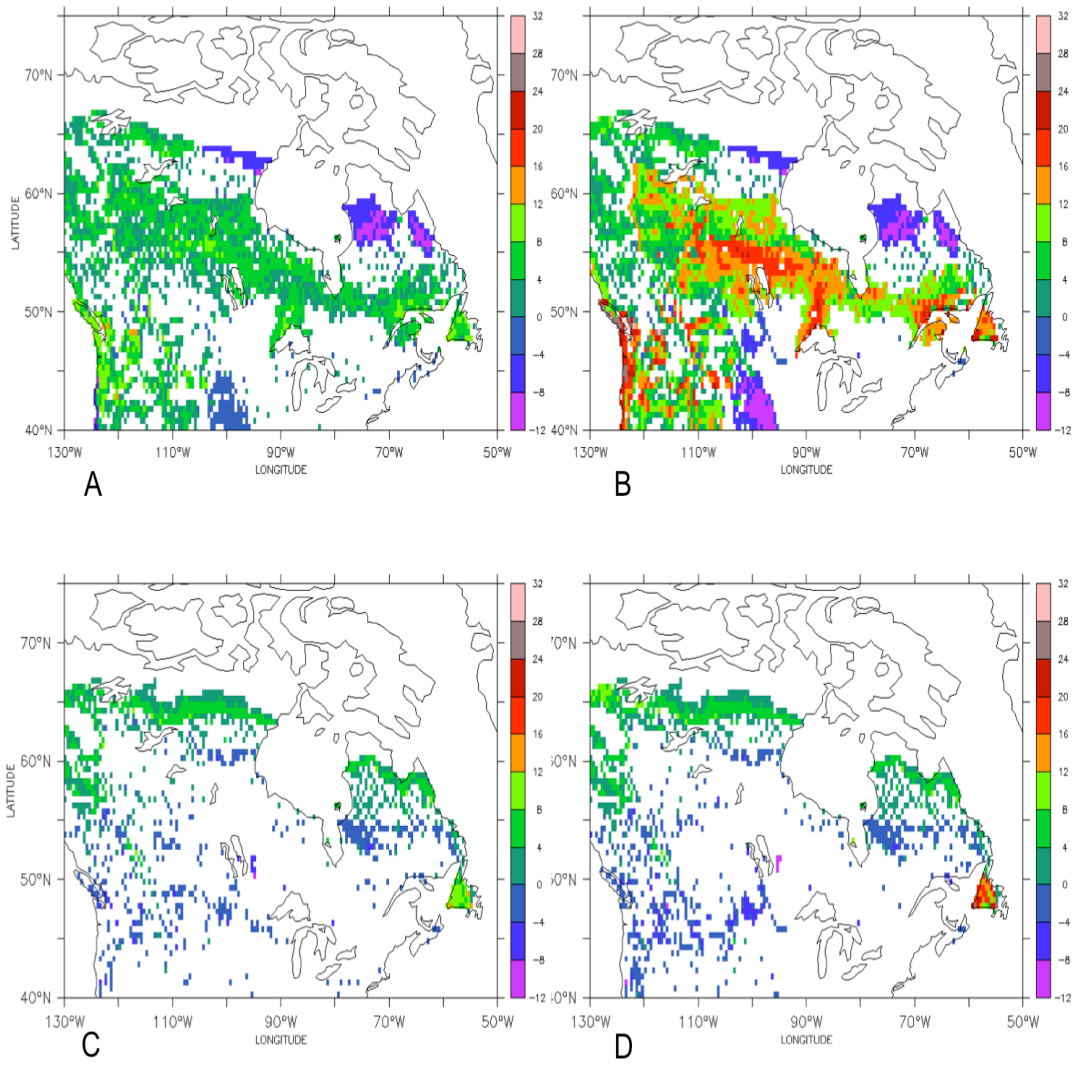

Figure 4.10. After 100 years the difference between the total carbon of a scenario and the predicted equilibrium carbon (A) is moderately higher except for the expected northern migration that hasn't occurred (purple). The difference between the scenarios evergreen carbon at year 100 and the predicted equilibrium value shows this is a consequence of the predicted future dominant PFT not having migrated yet (B). By simulation year 2000 total carbon (C) mostly matches equilibrium carbon except at the northern extent where migration supports forests that are unsustainable in the equilibrium scenario, and dominant PFT has been established as the evergreen total carbon (D) matches the total carbon (C) difference.

4.5 Discussion

This study used an advanced mechanistic ecosystem model that is pseudo-spatial, with a theoretical pseudo-spatial migration sub-model, and future climate data to perform a model experimental design on the effect of dispersal distance, dispersal mode, and disturbance rate on the transient response of vegetation and carbon redistribution over North America. Results suggest modest changes in total carbon as a result of larger changes in dominant PFT distribution. Future climate caused total carbon to overshoot the predicted equilibrium carbon before approaching, but remaining elevated, the predicted equilibrium response. This is caused by modest increases in biomass at evergreen sites that are predicted to switch dominant PFT to deciduous. High dispersal strategies correct for the most of this effect but total carbon remains elevated from migration supporting northern forests in areas that the equilibrium response would otherwise classify as non-forest as they are not self sustaining. Percentage of total carbon in the scenarios is typically higher than the predicted equilibrium total carbon, ranging from 94% to 116% of the equilibrium response with a mean value of 107%. This is from the combination of dominant PFTs not establishing at the equilibrium predicted extent from low dispersal strategies and expansion of the northern extent of forests. This combination also suppressed the percentage of sites whose dominant PFT matched the predicted equilibrium response, with sites matched ranging from 60% to 86% with a mean of 74%. The RMSE of the average effect for total carbon was relatively constant with dispersal mode at 9.04 ± 4.3%, disturbance rate at 7.49 ± 2.22%, and dispersal rate at 6.54 ± 3.19%. The average effect for dominant PFT establishment exhibited a wider range in effect with

dispersal rate at 14.13 ± 4.75%, disturbance rate at 7.81 ± 2.73, and disturbance mode at 3.77 ±2.3%.

This study, to our knowledge, is one of the first to examine the transient response of vegetation with an advanced mechanistic model at continental scales with multiple dispersal rates, dispersal modes, and disturbance rates. The computational requirement of simulating these interactions often leads to studies at the landscape to subcontinent scale, but the pseudo-spatial approach implemented here removed that restriction. Though novel in approach, our results are comparable to previous studies of the effects of dispersal, disturbance, and competition on carbon and vegetation redistribution from climate change.

Modest net changes in total carbon with larger underlying grid changes were found by Schaphoff *et al.* (Schaphoff et al., 2006). Using the LPJ-DGVM with five different general circulation models (GCMs) for a climate change scenario produced an average increase of 7.1% in vegetation carbon. However, they had boreal forests as a source whereas we find it to be a temporary sink. This could be a result of the climate change scenario they used, the IS92a. The atmospheric CO_2 value used for this research was 575ppm while they used 703pp. Bachelet *et al.* (Bachelet et al., 2001) used an equilibrium model, MAPSS, and a dynamic model, MC1, to simulate changes in potential equilibrium vegetation and carbon distribution in the US and found that moderate temperature increases produced an increase in carbon with limited redistribution but higher temperature changes produced widespread redistribution and carbon loss. Solomon and Kirilenko (Solomon & Kirilenko, 1997) used three climate scenarios to predict future equilibrium distribution carbon with and

without migration and found modest total gains in carbon were the product of larger underlying redistribution of ecosystems.

Disturbance can both accelerate and impede migration. Disturbance rates control the probability of new species establishment as some disturbance is needed for new species to enter an ecosystem but too much prevents establishment (Denslow, 1980; Emanuel et al., 1985). With increased disturbance we see the deciduous PFT migrate and establish faster (Figure 4.5) but also a decrease in the range of northern expansion (Figures 4.4 and 4.6). The MIGRATE model investigates how available habitat impacts migration rates and shows that increased suitable habitat increases migration rates (Collingham & Huntley, 2000). And FORSKA, a gap model, also showed increased disturbance lead to faster redistribution in the mixed conifer/northern hardwoods zone of northern Europe (Sykes & Prentice, 1995). Species are only so resilient to disturbance so increased disturbance in low biomass areas can impede migration (Iverson et al., 2011).

Migrations greatest influence will occur at plant functional type (PFT) transition zones, where evergreen forests are expected to migrate from the taiga into the tundra (Ranson et al., 2004) and deciduous forests are expected to move northward (Goldblum & Rigg, 2005). Northward migration of boreal species into regions previously classified as tundra is already occurring (Chapin et al., 2010) as remote sensing supports tree line advance (Grace, 2002). Both of these trends are represented, and boreal forest exists further north in scenarios with dispersal (Figures 4.3, 4.10).

This study has made important advances in using an individual based mechanistic model to predict the potential transient response of vegetation and carbon to climate change over large domains. Future work should prioritize expansion of the scenarios used and incorporate additional metrics. Only one climate change scenario was used, with a static value of CO_2 that is high, but not the highest presented in the SRES. The NARCCAP is producing numerous current and future climatologies with coupled RCMs and GCMs. As they are all forced with the A2 scenario a sensitivity analysis on the transient response can be performed. The atmospheric CO_2 concentration used in our mechanistic plant growth calculations can be increased. The pace of the change can be simulated. The disturbance rate can be PFT specific rather than equal for all types. Climate change is causing increased insect outbreaks that are damaging boreal forests (Kurz et al., 2008) so the disturbance rates here could be increased. Fire is also increasing and altering species distribution (Kasischke et al., 2010). ED has a fire model sub-model, as well as a landscape sub-model, that would impact the transient response An increased disturbance rate for only the evergreen species may allow deciduous establishment of dominant PFT in a shorter amount of time. A static dispersal distance was used but long distance dispersal is governed by the tail of dispersal kernels (Davis, 2001; Renton et al., 2013) and can be implemented. Additional PFTs can be used. To initialize and validate against remote sensing data deciduous and evergreen PFTs were used, but this can be expanded on. ED currently has seven total plant functional types, the others being two grasses and three tropical trees. The climatologies were at half-degree but could be downscaled and if future climatologies for other regions are generated they could be explored in a

similar fashion. This research presents a novel method to simulate the transient response of vegetation and carbon to climate change in large domains and future research should replicate many of the studies that have been conducted at smaller scales on disturbance, dispersal, competition, and landscape characteristics.

4.6 Conclusions

This study predicted the potential impacts of dispersal distance, dispersal mode, and disturbance rate on the transient response of vegetation and carbon to climate change in northern North America. The major conclusions are: (1) Relatively similar impact factors on carbon for dispersal rate, dispersal mode, and disturbance rate with modest net gains in total carbon for the majority of scenarios from (a) an increase in the northern extent of forests as sites that are not self sufficient under equilibrium conditions are maintained by continued migration into the site and (b) a slight increase in carbon at sites predicted to switch dominant PFT from evergreen to deciduous before the transition occurs. (2) PFT redistribution is strongly impacted by dispersal rate, moderately impacted by disturbance rate, and limitedly impacted by dispersal mode. These results support continued research on the impact of plant migration on vegetation and carbon redistribution from climate change at large domain scales with regards to additional climate change scenarios, PFT specific disturbances, fire, dispersal strategies, and other fine-scale processes.

Chapter 5: Conclusion

5.1 General Results

The objective of this research was to expand on previous research of the response of plant migration to climate change and the potential impact this has on vegetation redistribution and carbon sequestration potential but at continental scales.. Previous work on the equilibrium response has been done with both climate-ecosystem classification schemes and the use of DGVMs and shows a wide range in potential terrestrial carbon redistribution and sequestration potential dependent on both the model and climate change scenario used. Much less attention has been given in modeling studies to model validation of these estimates, and to the transient response, particularly at large scales. With growing national/international interest in carbon, and potentially accelerating climate change, the need to address these issues is high.

There are many challenges to addressing these questions with models. Perhaps most importantly, is the issue of scale: the domain of interest is large, but the detail and processes influencing the response are small/local. Even with advanced computers, brute force simulation of the individual plant processes of growth, mortality, dispersal, is prohibitive at large scales. The use of ED and its novel approach to scaling was essential to this research. Pseudo-spatial models like ED operate by laying a larger grid over the fine scale grid of the forest gap model and then combining the individuals of the underlying forest gap grid by size, age, and structure. This decreases computational time, which allows for larger domain

simulations and the model is still individually based, so dispersal and migration can be simulated. However, for spatially explicit processes like dispersal this presents a challenge given the explicit location of individual trees within the larger grid cells is no longer known. Therefore a method to simulate the spatially explicit process of dispersal in a pseudo-spatial framework was essential to be developed.

Three major objectives emerged that became the basis of the chapters in this dissertation. (1) The current distribution of dominant PFTs needed to be validated with remote sensing data and a future climatology used to verify that the equilibrium response warranted further research into the effects of the transient response. (2) A method for simulating the spatially explicit process of dispersal in a pseudo-spatial framework was derived and inserted into an advanced, mechanistic pseudo-spatial model (ED) that allowed for large domain simulation. (3) The transient response of plant migration was then observed under varying dispersal distances, dispersal modes, and disturbance rates to determine the potential impact on vegetation and carbon redistribution from climate change. A detailed review of each component is provided in the following section.

5.2 Summary of Findings

This research examined the impact of plant migration from climate change on vegetation distribution and carbon sequestration potential from climate change. Each chapter builds off of the previous one to achieve the ultimate goal of large domain simulation of the transient response of vegetation to climate and the impact this may have on potential carbon sequestration. The major findings were:

- As the result of Cal/Val, ED model predictions of dominant PFT distribution over North America matched remote sensing classification at 76% of 3064 sites classified as forest by remote sensing (Chapter 2).
- The equilibrium forest response to a future climate change scenario had total net forested area in northern North America increase by 2% and the net carbon sequestration potential increase by 8% (Chapter 2).
- The net equilibrium forest response to a future climate change scenario had large underlying gross changes. Deciduous cover expanded by 77% and gained 107% of its current carbon sequestration potential while evergreen cover decreased by 55% and lost 31% of its current carbon sequestration potential. 60% of northern North America was predicted to change dominant PFT and the percentage of terrestrial carbon sequestration potential attributed from evergreen and deciduous PFTs changed from a 3:1 to a 1:1 ratio with a wide range in site level fluctuations (Chapter 2).
- The spatially explicit process of plant migration can be modeled in a pseudo-spatial environment using a theoretical equation dependent on dispersal distance, site size, area of the site occupied, and the number of seeds produced (Chapter 3).
- The theoretical equation for pseudo-spatial plant migration produced expected results in the non-idealized environment of an advanced mechanistic model (ED) with prior knowledge of the soil and climate gradients at the test sites (Chapter 3).

- After 2000 simulation years with varied dispersal modes, dispersal rates, and disturbance rates, percentage of total carbon sequestration potential with respect to the equilibrium scenario ranged from 94% to 116% with a mean value of 107% and dominant PFT distribution ranged from 60% to 86% with a mean of 74% (Chapter 4).
- Carbon sequestration potential tended to be higher than the predicted equilibrium value as (1) sites classified as evergreen under current climate but predicted to switch dominant PFT to deciduous under future climate supported slightly higher biomass before the switch occurred and (2) the northern extent of forests increased as sites that were not self sustaining were instead supported by additional individuals migrating (Chapter 4).
- Dominant PFT distribution tended to be lower than the predicted equilibrium value as (1) only 10km dispersal was a high enough dispersal rate for the deciduous PFT to migrate into the entire predicted range and (2) the expansion of the northern evergreen extent of forests (Chapter 4).
- The time scale for vegetation redistribution to reach the predicted equilibrium response is on the order of centuries and strongly dependent on dispersal and disturbance rates (Chapter 4)
- Increased disturbance accelerated migration in high biomass areas but reduced forest extent in low biomass areas (Chapter 4).
- Plant migration from climate change had a high impact on the redistribution of vegetation but a moderate impact on the carbon sequestration potential (Chapter 4).

5.3 Future Research

Future research is needed to extend the gains from this thesis and advance on the goal of this research. Areas for future work fall into two broad categories: additional model advances, and evaluating of additional climate scenarios. For ED much of the work that has been conducted at the sub-continent scale by forest gap models should be replicated at this increased domain to provide a variety of estimates on how plant migration from climate change impacts vegetation distribution and carbon sequestration potential. This can include additional PFTs, species-specific disturbance and dispersal rates, and the impact of fire and landscape fragmentation on migration rates. For climate, additional scenarios should be evaluated. Additional scenarios are available from the NARCAAP that would allow for a range of alternative future climate conditions to be considered and expanded to better understand how CO_2 concentrations effect vegetation distribution and carbon sequestration potential. The inherent difficulty in calibrating and validating a future prediction means a robust range of scenarios should be run to bracket potential effects. This research demonstrated the ability to simulate the transient response of plant migration at continental scales, and future research should attempt to replicate many of the studies that have been conducted at the landscape scale in this increased domain size to determine a robust range for the potential impact of plant migration on vegetation and carbon redistribution from climate change.

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